

THE LEAF ENERGY BALANCE OF A DESERT PLANT
CITRULLUS COLOCYNTHIS (L.) SCHRAD.
WITH SPECIAL REFERENCE TO WATER ECONOMY

By

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DEDICATION

This thesis is dedicated to my parents and wife

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DECLARATION

This thesis has been composed by myself and it has not been submitted in any previous application for a degree. Results reported within are from my own work except where acknowledged to the contrary.



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LIST OF SYMBOLS AND ABBREVIATIONS

A	= leaf plan area or area (m^2)
AW	= all-wave radiation sensed with a radiometer (W m^{-2})
b	= specific heat of brass ($\text{J g}^{-1} \text{ } ^\circ\text{C}^{-1}$)
C	= rate of sensible heat transfer by convection (W m^{-2})
C_p	= specific heat of air at constant pressure ($\text{J g}^{-1} \text{ } ^\circ\text{C}^{-1}$)
c	= root length conversion factor
D	= thermal diffusivity of dry air ($\text{m}^2 \text{ s}^{-1}$)
d	= characteristic dimension of leaf (m)
E	= calculated transpiration rate ($\text{g m}^{-2} \text{ s}^{-1}$)
E_o	= observed transpiration rate ($\text{g m}^{-2} \text{ s}^{-1}$)
e_a	= water vapour pressure in the ambient air (mbar)
e_L	= saturated water vapour pressure at the leaf temperature (mbar)
F	= spectral energy flux (W m^{-2})
g_a	= aerodynamic/boundary layer conductance (m s^{-1})
g''_a	= aerodynamic/boundary layer conductance when twice the plan area is taken into account (m s^{-1})
g_s	= stomatal conductance (m s^{-1})
H	= total length of straight lines in root survey (cm)
h_c	= heat transfer coefficient ($\text{J m}^{-2} \text{ s}^{-1} \text{ } ^\circ\text{C}^{-1}$)
L	= longwave radiation flux (W m^{-2})
L_A	= leaf area (cm^2)
L_d	= downward longwave radiation flux (W m^{-3})
LR	= root length (cm)
L_w	= leaf dry weight (g)
m	= slope of the plot of $\ln \Delta T$ against time
n	= number of root interceptions with a grid or straight line
Rn	= net radiation (W m^{-2})
r	= resistance to diffusion of entity (s m^{-1})
r_a	= aerodynamic/boundary layer resistance denoted by superscript as to diffusing entity (s m^{-1})
r_{cu}	= cuticular resistance (s m^{-1})
r_s	= stomatal resistance (s m^{-1})
S	= shortwave radiation flux (W m^{-2})
SLA	= specific leaf area ($\text{cm}^2 \text{ g}^{-1}$)
SMC	= soil moisture content (%)

IV

SVPD = saturation vapour pressure deficit (mbar)
SW = shortwave radiation sensed with a solarimeter (W m^{-2})
 ΔT = temperature difference ($^{\circ}\text{C}$)
 T_a = air temperature ($^{\circ}\text{C}$)
 T_L = leaf temperature ($^{\circ}\text{C}$)
 T_L^* = non-transpiring leaf temperature ($^{\circ}\text{C}$)
VPD = leaf-air vapour pressure (mbar)
 u = wind speed (m s^{-1})
WBD = depression of the wet bulb

GREEK LETTERS

α = fraction of incident energy absorbed by a leaf
 ν = kinetic viscosity of dry air ($\text{m}^2 \text{s}^{-1}$)
 γ = psychrometric constant ($0.66 \text{ mbar } ^{\circ}\text{C}^{-1}$)
 λ = latent heat of vapourisation
 π = 3.142
 ρ = density of air (g m^{-3})
 σ = Stefan-Boltzmann constant ($5.67 \times 10^{-8} \text{ W m}^{-2} \text{ K}^{-4}$)
 Σ = sum of series
 ψ = leaf water potential (MPa)

ABSTRACT

It was the aim of this study to investigate the water relations of a desert cucurbit *Citrullus colocynthis*. This species uses much water in transpirational cooling even though water in the desert is in short supply. Energy balance theory was used in conjunction with the measurement of the leaf temperature and other climatological parameters, to estimate the transpiration rates and the leaf surface conductances.

C. colocynthis leaves did indeed display high transpiration rates and frequently had temperatures cooler than the ambient air. In comparison with desert plants, *Citrullus* has relatively high stomatal conductance and a low boundary layer conductance in ordinary conditions. The lethal temperature of the plant is rather low in relation to other desert plants, being around 50 °C though some kind of damage does occur at even lower temperatures. By its high transpiration rate, the plant avoids lethal temperatures. The transpirational cooling is not always displayed. It seems probable that this response is only displayed in the hottest part of the year. The plant has the ability to grow tap roots which penetrate deep into the water table to sustain the rate of transpiration. The transpiration rate and leaf cooling is sensitive to radiation interception which to some extent is under control through stomatal response and aerodynamic changes. Preliminary calculations suggest that vegetation containing *Citrullus* and similar species may consume significant quantities of water which otherwise could be available to field crops.



Citrullus colocynthis (L) Schrad. in its natural habitat.
Note the vertical posture of most of the leaves.

CHAPTER 1

INTRODUCTION

Plants living in the desert regions of the world must be able to withstand a wide range of stresses. The most important stresses are probably those that are the direct or indirect consequence of the high solar radiation flux, associated with long periods without rain. Unadapted species would not be able to survive the water stress that would develop within their tissues, nor the temperature attained in the middle of the day.

In order to survive, desert plants thus display a wide range of adaptations at all levels of their organisation: structural, anatomical, physiological and biochemical. Although classical studies originally drew attention to the anatomical features associated with the conservation of the water, like thick cuticles and sunken stomata (e.g. *Retama raetam* and *Haloclon salicornicum*), it was realized quite early by some people that many desert plants, paradoxically, have a high rate of transpiration (Maximov, 1929).

1.1 Transpiration rates in desert plants

Since water is scarce in deserts one would think that plants growing there would display low transpiration rates, and indeed this is true in many cases and especially in desert succulent plants, as reported by numerous workers (e.g.

Migahid, 1954; 1961; Petrov, 1976; Stocker, 1976).

"It is erroneous to suppose that desert plants of necessity transpire very slowly. Many investigators state that branches of such typical desert plants as *Alhagi camelorum* or *Citrullus colocynthis* wilt immediately on being detached from the plant." (Maximov, 1929).

This is consistent with the view that a high rate of transpiration does sometimes occur. Zohary (1962) reported plants of high transpiration rate such as *Prosopis*, *Alhagi* and *Tamarix*. High transpiration was also reported for some trees growing in the desert such as *Acacia raddiana* and *A. spirocarpa* (Evenari, Shanan & Tadomer, 1971). They also reported high transpiration in the biseasonal annuals such as *Salsola intermix* and *S. valkensii*. Table 1.1 contains values of transpiration rates for some desert plants from different environments, some of which have high transpiration rates. These rates, when converted to units of energy flux, are substantial and suggest that the leaf energy balance may be dominated by the evaporation component.

1.2 Types of desert plants on the basis of leaf temperature

Lange (1959), after his trip to the Mauritania desert, classified desert plants into three groups:

1. Under-temperature plants

Author	Species	Location	Trans. Rate $\text{g m}^{-2} \text{s}^{-1}$	Trans. Rate as an energy flux (wm^2)	Leaf size (cm)	Leaf conduct- cms^{-1}
Lange (1959)	<i>Salvadora persica</i>	Mauritania	0.018	43		
" "	<i>Capparis decidua</i>	"	0.063	151		
" "	<i>Calotropis procera</i>	"	0.06	144		
" "	<i>Leptadenia pyrotechnica</i>	"	0.118	283		
" "	<i>Chrozophora senegalensis</i>	"	0.241	581		
" "	<i>Abutilon muticum</i>	"	0.091	218		
" "	<i>Citrullus colocynthis</i>	"	0.15	363		
Pearcy et al (1974)	<i>Phragmites communis</i>	Death Valley	0.21-0.23	505-553		0.5-0.4
Stocker (1976)	<i>Capparis spinosa</i>	Sahara	0.022*			
"	<i>Peganum harmala</i>	"	0.033*			
"	<i>Citrullus colocynthis</i>	"	0.044*			
Smith & Nobel (1977b)	<i>Hypris emoryi</i> (sun leaves)	Palm Desert	0.05	117		0.83
Smith (1978)	<i>Encelia farinosa</i>	Sonoran Desert	0.11-0.25	264-601	3.6-8.2	0.54-2.0
" "	<i>Datura melaloides</i>	" "	0.16-0.22	384-529	4.3-9.7	0.6-1.8
" "	<i>Eriogonum inflatum</i>	" "	0.14-0.23	336-553	4.0-7.0	0.47-1.4
" "	<i>Larrea tridentata</i>	" "	0.03-0.14			0.09-0.23
" "	<i>Ambrosia dumosa</i>	" "	0.04-0.14	96-364	<1.0	0.11-0.31
" "	<i>Hymenoclea salsola</i>	" "	0.02-0.09	48-216	<1.0	0.08-0.27
" "	<i>Opuntia basilaris</i>	" "	<0.012	28	7.4-16.2	<0.01
" "	<i>Opuntia bigelovii</i>	" "	<0.007	16.8	3.1-5.4	<0.02
" "	<i>Echinocactus acanthoides</i>	" "	<0.01	24	15.0-23.2	<0.02

* Values averaged over a 24h period

TABLE 1.1: Transpiration rate for several desert plants from different environments.

In this group, plants have relatively large leaves which in bright sunshine remain remarkably cooler than the ambient temperature especially during the hottest hours of the day. This cooling is the consequence, at least in part, of a high transpiration rate. Examples are *Citrullus colocynthis* and *Perqularia tomentosa*.

2. Over-temperature plants

Leaves of these plants in full sunlight remain at a higher temperature than the ambient. Transpiration rate in this group was not sufficient to lower substantially the leaf temperature. Examples of this group are *Salvadora persica*, *Zygophyllum fortansii* and *Phoenix dactylifera*. Leaf temperatures as much as 13°C above that of the air were measured.

3. Neutral plants

Leaf temperatures in the last group were not far from the surrounding temperatures and transpiration was insufficient to cool leaves below the ambient. These temperatures remained slightly above that of the air. Examples of this group are *Capparis decidua* and *Leptaderia pyrotechnica*. These can be referred to as 'neutral plants', a term embracing plants in which leaf temperature is always within a few degrees of air temperature.

Since Lange (1959), several workers have measured leaf temperatures of desert plants in various environments, broadly confirming Lange's classification.

Phragmites communis (Death Valley) was able to reduce its leaf temperature to 5-8 °C below that of the air (Pearcy, Berry & Bartholomew, 1974), combining this with a high transpiration rate and maximum leaf conductance of 0.5 cm s⁻¹. Smith (1978) measured leaf temperature of *Encelia farinosa* (in the Sonoran Desert) which had temperatures as low as 18 °C below the ambient, with stomatal conductance of 0.54-2.0 cm s⁻¹ at an air temperature of 43.6 °C. 'Over-temperature' plants have been found among cactus species. Gates, Alderfer and Taylor (1968) measured leaf temperatures of 10-16 °C above the air temperature in some *Opuntia* sp. (in Utah). An extreme case was recorded by Smith (1978) when, in the Sonoran Desert, leaf temperature of *Opuntia basilaris* was 20 °C above the air temperature and leaf conductance was only 0.01 cm s⁻¹. 'Neutral plants' were found in the two sites, Utah and the Sonoran Desert. In general, small leaves were within 3 °C of air temperature (Gates et al., 1968; Smith, 1978).

1.3 Morphological and physiological determination of the leaf temperature

The partition of energy between transpiration and convection is determined by the stomatal frequency, size and the degree of opening of the pores, and these are likely to be the crucial features in determining whether a plant is 'under-temperature' or 'over temperature'. The partition of energy also depends on leaf shape, size and orientation (Drake, Raschke & Salisbury, 1970). In most desert plants, leaves are

small as an adaptive feature because the smaller the leaf, the larger the convection coefficient and the less likely the leaf is to become overheated. Such a leaf can be described as being coupled strongly to the air temperature (Campbell, 1977; Gates, 1980).

On the other hand, desert plants with large leaves or other organs will have a smaller convection coefficient, and therefore be susceptible to heating to a temperature exceeding the surroundings, as in the case of the cactus species which have their stomata shut during day time. But other desert plants with relatively large leaves have their stomata open and so exhibit a different behaviour as already mentioned: most of them become cooler than the air.

Since some desert plants transpire at high rates, it is not surprising that many have high stomatal numbers. Sen (1973) reported stomatal frequency and size of 45 species growing in the Indian desert. Such frequencies are not regarded as constants for the species, the number of stomata may depend on the seasonal variations in growing conditions. Sen and Bhandari (1974) reported that in *C. colocynthis* stomata number per unit area was low when growth had been retarded by cold; but in hot months after fresh growth of new leaves, stomatal number increased. The maximum stomatal frequency and aperture occurred in the rainy season. It is instructive to compare Sen's data with those of Meidner and Mansfield (1968) for more mesic species (Table 1.2). It can be seen that some desert plants indeed have a high stomatal frequency.

The leaf temperature must also depend on the receipt and

Author	Group	Range		Size: length in μm	
		lower surface	upper surface	lower surface	upper surface
Meinder & Mansfield (1968)	Temperate ferns	59-85	-	21-38	-
	Conifers	16-120	14-120	12-24	
	Temperate Crops	45-175	50-175	16-28	
	Temperate Trees	170-370	-	10-13	
Sen (1973)	<i>Colotropis procera</i>	184	210	27	24
" "	<i>Cucumis sativus</i>	684	578	15	18
" "	<i>Indigofera linifolia</i>	315	526	15	15
" "	<i>Citrullus colocynthis</i>	578	315	30	33
" "	<i>C. lanatus</i>	184	421	27	27
Althawadi (unpublished)	<i>C. colocynthis</i>	300	235	13.8	14

TABLE 1.2: Shown stomatal frequency mm^{-2} for the desert plant *Citrullus colocynthis* compared with mesic species.

absorptance of radiation. Plants not possessing any means to reduce radiation load may suffer heat damage. One such means is the high reflectance that is produced by wax deposits, hairs and spines. Another is the adoption of a favourable leaf posture. Most desert plants either hold their leaves vertically or undergo alterations in leaf angle whenever they are exposed to high radiation particularly in the middle of the day.

Gates (1980) reported leaf temperatures of *Erythrina indica*; those leaves which were standing vertically had temperatures 6 °C cooler than the horizontal ones. Other workers have also reported this phenomenon for desert plants (Sen, Chawan & Sharma, 1972; Pearcy et al., 1974).

1.4 General statement of the problem to be investigated

Although many workers have reported substantial cooling associated with high transpiration rates in desert plants, there are few detailed studies of the water economy of such species. Important questions to be asked include:

1. Why is so much water used when water is in such short supply? Lange (1959) suggested that water was transpired to cool the plant, avoiding lethal temperatures. If this is so, it may be economical to use water only 'in an emergency' when critical conditions are approaching. At all other times transpiration rates should be low to conserve water. If so, how is the high degree of control achieved?
2. How are the water supplies obtained? Is the root system especially deep or far spreading, and if so, is the growth rate of the plant reduced as a result?
3. How is the partitioning of the energy between evaporation and

convection controlled? To answer this question, it will be necessary to study the energy balance in detail, in relation to the surface resistances imposed by the stomata and the boundary layer.

It was decided that such questions would best be answered by studying one species in detail.

1.5 Choice of species

The Saudi Arabia desert is one of the most extensive in the world, occupying most of the country's area which is 220 million hectares. Its flora, described by Migahid (1978), comprises at least 600 species, several of which are known to be amongst those referred to as 'under-temperature' types by other workers. These include *C. colocynthis* and *Perqularia tomentosa*. Of these species, *C. colocynthis* was chosen as it occurs widely, its seeds are easy to collect and germinate, and it has already been studied to some extent. Moreover, it is a medicinal plant of antiquity, still used by bedouins (Zohary, 1962; 1982; El-sheik, 1982).

1.5.1 Ecology of *C. colocynthis*

Citrullus colocynthis is a summer-active plant, a perennial cucurbit distributed widely in hot dry regions in Asia and Africa (Lange, 1959; Shishkin, 1972), and Spain (Bhandari, 1978). It colonises sandy soil in deserts, especially depressions and wadis or places where ground water is not far from the soil surface.

It is a creeping plant in its native habitat, radiating

branches on all sides to a distance of a few meters. The plant leaves are deeply lobed, narrowly triangular, with a length of 4-8 cm and 4-5 cm wide. It produces fruits the size of an apple at the end of the summer season.

The plant dies back in the winter, surviving as rootstock, as the seed germination in nature is poor (Koller *et al.*, 1963). Its growth starts after the rainy season, producing flowers in the late summer. Growth is retarded by the winter cold.

1.5.2 'Under-temperature' *C. colocynthis*

Lange (1959) noted the ability of the plant to regulate its leaf temperature far below air temperature. Leaf temperature was recorded during two consecutive warm dry days in Timzak (Mauritania). Soil temperature was over 70 °C and the creeping horizontal shoots were 1-2 cm above the soil surface. The leaf temperature in the morning was 10 °C cooler than the air. In the early afternoon when air temperature was 53.7 °C the leaf temperature was only 41 °C. When the leaf next to the previous one was cut off at midday its temperature rose up to 60 °C in 30 min. On the next day a similar temperature cycle could be repeated with another plant. In another location (Grara) with an ambient temperature of 44 °C the leaf was 3.2 °C cooler than the air. In all cases the leaf temperature did not exceed 42.5 °C. Lange ascribed the ability of the plant to lower its organs' temperature far below that of air to the extremely high transpiration rate. Thus *C. colocynthis* may be regarded as a classic 'under-temperature' desert plant, on the basis of Lange's work on leaf temperature and Sen's observations on stomatal

numbers.

1.6 Outline of thesis in relation to objectives

In Chapter 2, I have shown how measurement of leaf temperature together with certain other parameters, lead to a solution of the leaf energy balance to obtain transpiration rates and stomatal conductance. I have used this technique extensively in my work as it is adaptable and can be used in the field.

Chapter 3 consists of two parts; the first part will be devoted to verification of the theory of the leaf energy balance. In the second part, I report an experiment in which the environment of the plant was progressively warmed, in daily steps, whilst the transpiration and stomatal and boundary layer conductances of the plant leaf were calculated from the leaf temperatures.

Discussion of crucial physical attributes of the plant, especially aerodynamic resistance and leaf optical properties are reported in Chapter 4.

In Chapter 5 an attempt is made to investigate the effect of temperature on leaf movement at different levels of soil moisture.

An experiment on the plant growth and the development of the root system under different levels of soil water table is reported in Chapter 6.

In Chapter 7 an experiment to determine the lethal temperature of the plant leaves will be reported.

Measurements of stomatal conductance, transpiration rate and the leaf boundary layer conductance for *C. colocynthis* in its native habitat are reported in Chapter 8.

An overall, general discussion and conclusions are given in Chapter 9.

CHAPTER 2

SOLVING THE ENERGY BALANCE OF LEAVES: THEORY AND PRACTICE

The relationship between leaf temperature and the environment depends on the absorption of energy, and the partition of that energy between transpiration and other energy-dissipating processes.

A number of authors have discussed the energy balance of plant leaves (e.g. Raschke, 1960; Gates, 1964; 1968; 1980; Linacre, 1967; 1972; Monteith, 1973) and some have shown how leaf temperature can be calculated from a knowledge of the appropriate environmental and plant variables (e.g. Gates & Papian, 1971; Campbell, 1977).

In the present work it was intended to apply the energy balance equations so as to use the knowledge of leaf temperature to derive the transpiration and convection rates from single leaves. A similar approach has been used by Impens *et al* (1967) and Thorpe and Butler (1977).

2.1 Theory

The first law of thermodynamics states: energy can neither be created nor destroyed, but only converted from one form to another.

Applying this law to a plant leaf in an environment with various sources of energy transfer, the energy balance of the leaf would be:

Energy Gains = Energy Losses + Energy Storage

or, more specifically:

$$R_n = \lambda E + C + G + P + S \quad (2.1)$$

Where R_n = is the net heat gain from radiation (shortwave and longwave)

λE = loss of latent heat by evaporation (λE is found by multiplying the rate of water loss E [E , units $\text{g m}^{-2} \text{ s}^{-1}$] by the latent heat of vaporization [the value of λ at 20°C is 2454 J g^{-1}])

C = loss of sensible heat by convection

G = conduction of heat down the petiole, or through contact between leaf and soil

P = the rate at which energy is being trapped in chemical bonds by photosynthesis

S = the rate at which heat goes into storage within the leaf.

(All terms are in appropriate units of energy flux, W m^{-2}).

G , quantitatively, is normally minute. P , the transfer of radiant energy to chemical bonds, is usually less than 3% of the total leaf energy budget. S , generally, is small except for massive organs such as cactus stems. Therefore these terms (G , P and S) can usually be ignored (Gates & Papian, 1971; Monteith, 1973; Grace, 1983; Jones, 1983). Thus the energy that is absorbed by a leaf will be dissipated through two main processes, evaporation and convection. So we can rewrite the equation (2.1) in the form:

$$R_n = \lambda E + C \quad (2.2)$$

The net radiation (R_n) is the balance between the total incoming flux of radiation and the outgoing flux due to reradiation and reflection. It is composed of the shortwave radiation (S), the visible and the near infra-red part of the waveband (400 - 3000 nm), and the long wave radiation (L). The flux density of longwave radiation reradiated from the leaf can be found by applying the Stefan-Boltzmann law assuming that the leaf behaves like a perfect black body, i.e. that longwave radiation is equal to σT_L^4 . Where T_L is the absolute leaf temperature (in degrees Kelvin), σ is Stefan's constant ($5.67 \times 10^{-8} \text{ W m}^{-2} \text{ K}^{-4}$). Using the subscript i for into the leaf and o for out of the leaf:

$$R_n = L_i - \sigma T_L^4 + S_i - S_o \quad (2.3)$$

The evaporation rate λE is driven by the gradient of water vapour pressure between leaf and air $e_L - e_a$, where e_L is the saturated water vapour pressure at leaf temperature (mbar) and e_a is the vapour pressure (mbar) in the surrounding air. Since λE is restricted by the stomatal resistance r_s and the boundary layer resistance r_a (Monteith, 1965) :

$$\lambda E = \frac{\rho C_p (e_L - e_a)}{\gamma (r_s + r_a)} \quad (2.4)$$

The physical constants ρ , C_p and γ bring items on the right hand side to the appropriate units of W m^{-2}

Where ρ = density of air (1150 g m^{-3})

C_p = specific heat of air ($1.01 \text{ J g}^{-1} \text{ }^\circ\text{C}^{-1}$)

γ = psychrometric constant ($0.66 \text{ mbar }^\circ\text{C}^{-1}$)

Referring back to equation (2.2), the rate at which energy is dissipated by convection (C) is expressed by a simple equation. Since C is proportional to the difference between leaf temperature and air temperature ($T_L - T_a$), it is restricted only by the boundary layer resistance r_a . So:

$$C = \frac{\rho C_p (T_L - T_a)}{r_a} \quad (2.5)$$

Water vapour and heat diffuse through the same boundary layer, but r_a for heat and r_a for water vapour are not numerically quite the same because of the difference between the diffusivity of heat and water vapour (Grace, 1981). However, in the special case of diffusion through the boundary layer, the difference is small and for practical purposes can be ignored.

Now let us consider an actively transpiring leaf: so

$R_n = \lambda E + C$ or, writing the terms in full:

$$L_i - \sigma T_L^4 + S_i - S_o = \frac{\rho C_p (e_L - e_a)}{\gamma(r_a + r_s)} + \frac{\rho C_p (T_L - T_a)}{r_a} \quad (2.6)$$

Next we consider the same leaf in which transpiration has been stopped (i.e. $\lambda E = 0$). The new leaf temperature is T_L^* , instead of T_L , therefore:

$$L_i - \sigma T_L^{*4} + S_i - S_o = 0 + \frac{\rho C_p (T_L^* - T_a)}{r_a} \quad (2.7)$$

When (2.7) is subtracted from (2.6) the result is:

$$\sigma(T_L^{*4} - T_L^4) = \lambda E + \frac{\rho C_p (T_L^* - T_a)}{r_a} \quad (2.8)$$

The surface temperature can be measured with a thermocouple. The net radiation (Rn) which is absorbed by the leaf can be measured with a miniature net radiometer or calculated from a knowledge of the longwave and shortwave fluxes together with the leaf optical properties; and r_a can be found by rearranging equation (2.7). Putting the r_a value into equation (2.6) and rearranging the two sides of the equation to put E alone, enables E to be determined. Measuring Rn will then enable us to find C in equation (2.2). As e_a can be measured, and e_L is found from tables when T_L is known, it is possible to calculate the value of r_s for the actively transpiring leaf by rearranging equation (2.4). A computer program was used to do all these calculations (Appendix A).

2.2 Practice

Leaf surface temperature is a crucial variable in this approach, and a high degree of precision in its measurement is required. There are three types of temperature sensors currently used for this purpose:

- 1) The infra-red thermometer, which is based on the Stefan-Boltzmann black body law, is satisfactory and capable of resolving a 0.5°C difference; but errors can be encountered since its field of view is usually large ($>2^{\circ}$) and it thus views other sources of radiation behind the leaf (if the leaf is small), or if placed too near the leaf, may itself modify the energy balance through shading. Moreover it requires a calibration and determination of the response time before usage (Woodward & Sheehy, 1983).
- 2) Leaf temperature could also be measured by various types of resistance thermometers such as thermistors which are semi-conductors whose resistance changes with the temperature. These sensors have some disadvantages such as their nonlinearity, and the fact that even the smallest size ($\approx 1\text{ mm}$) is too large to use for measuring leaf surface temperature because it would cause local disturbance of the leaf boundary layer.
- 3) The most common sensors are thermocouples which are cheap and easy to construct, and their junction can be very small. Because of this, copper-constantan thermocouples 0.1 mm in diameter (SWG 42, Dural Plastics, Australia) were used for measuring the temperature of the leaf surface throughout this study.

The connection between the sensor and the surface is also of importance. Neither the leaf boundary layer nor the leaf optical properties should be changed when the leaf

temperature is being measured. Workers have tried different methods to achieve a good contact between the sensor and the leaf surface. Perrier (1971) reported several methods, such as winding the thermocouple wire along the leaf petiole and positioning the sensor to be in contact with the lower surface of the leaf. Although the leaf energy balance is hardly disturbed, only a poor contact is made between the sensor and the leaf surface. Others used a clip such as that described by Lange (1959; 1965). This clip makes good contact but it causes disturbances to the leaf boundary layer and it introduces conduction of heat between it and the leaf. This kind of clip was modified by embedding the thermocouple in Araldite. A third kind of contact is to use a frame with thin wires to hold the thermocouple in close contact with the leaf surface. This frame is meant to minimize disturbance to the leaf boundary layer characteristics and heat conduction, but it does cause pressure and could cause closure of some of the stomata. Some workers tried to attach the thermocouple wire directly by threading it through the leaf (Mellor, Salisbury & Raschke, 1964; Steiner, Kanemasu & Hasza, 1983). Taping of the sensor junction onto the leaf surface was used by some investigators (e.g. Impens *et al.*, 1967). Schulze *et al.* (1980) suggested pressing the end of the sensor onto the leaf tissue. The pressing method was also used by Smith (1978). A disadvantage of both threading, or to a lesser extent pressing, methods is the under estimation of the leaf temperature due to the leaf tissue wetness. Although most workers tried several techniques to minimize any change of the leaf aerodynamic

resistance or any local disturbance to the leaf tissue (subsequently some of the stomata might be shut), such caution cannot eliminate all influence of the attaching material.

It was decided in the present study to use sellotape glue extracted in chloroform to attach the junction and some of its leads to the leaf surface (Dixon, 1982). This provides a firm bond, and the presence of glue on the metal presumably confers black body properties onto the sensor so that radiative coupling as well as conductive coupling occurs. The method appears to have been first suggested by Digby Idle (Grace, pers. comm.).

2.2.1 Radiation

Net radiation can be either measured directly using a miniature net radiometer situated above and below the leaf. Alternatively, if the optical property of the leaf is known and the short and longwave radiation fluxes are also known, the radiation absorbed can be found by calculations.

2.2.2 Air temperature

For accurate measurement of air temperature in conditions of high energy flux, precautions are required to reduce radiative heating. Two approaches are possible: a) using a very small thermocouple in which convective dissipation of heat is very efficient and b) employing an aspirated radiation shield such as that in Assman psychrometer. Both of these approaches are discussed by Szeicz (1975) and Fritschen and Gay

(1979).

2.2.3 Humidity

Water vapour in the air can be measured with the humidity sensors such as the hygrometers which are available on the market nowadays-or by the dry and wet bulb method which is widely used. The latter method is usually considered more satisfactory and reliable (Etherington, 1982) particularly for field measurements. The two bulbs should be shielded and adequately ventilated. Discussion of these instruments are available in Szeicz (1975) and Fritschen and Gay (1979). The precision with which these variables must be measured depends on the case concerned. This point will be returned to in a later section.

CHAPTER 3

THE TRANSPIRATION RATES AND STOMATAL CONDUCTANCES OF LEAVES IN CONTROLLED ENVIRONMENTS

In Chapter 1 it was reported that the leaf temperature of *C. colocynthis* can often be lower than that of the ambient air. The work described in this chapter was designed to confirm this observation; and by applying the energy balance theory outlined in Chapter 2, to go further and evaluate the magnitudes of the stomatal and aerodynamic resistances involved in the response.

The first part of the chapter is concerned with verifying the method (Experiments 1 & 2). The second part reports an investigation conducted in a controlled environment (Experiment 3), in which temperatures, transpiration rates and the exchange resistances were all found during a period of several days over which the air temperature was progressively increased.

3.1 Materials and methods

The experiments were carried out in a growth cabinet (Model EF7, Controlled Environments, Canada) with illumination from seven 48 VHO fluorescent lamps and four 60 W incandescent lamps (Experiments 1 & 3), and in a Fisons cabinet (Model 2340 G3 Horizontal) with illumination from 21 high

intensity Wotan HQ1-R lamps and 12 pearl bayonet tungsten lamps (Experiment 2).

Seeds of *C. colocynthis* (Wadi Fatma, Saudi Arabia origin) were germinated by soaking them in water for 24 hours then applying a mechanical force on the seed coat to crack it along the suture (Koller et al., 1963). The seeds were germinated in petridishes at a temperature of 28-30 °C. When the radicle had emerged the germinating seeds were transferred to pots (10 x 8 cm containing 70% fine sand and 30% garden soil and added nutrients, with pH 7.3). Seedlings were grown for 6 weeks at an ambient air temperature 30 °C.

On all experiments newly-matured leaves were selected which were similar in appearance and fully expanded, showing no signs of senescence. The thermocouple junction was attached to the abaxial surface of the leaf parallel with the main vein using sellotape glue as described in Chapter 2. Thermocouples were referenced to the dry bulb of an electric Assman psychrometer which was placed within the room to sample air from around the plants. The signals were amplified using microvolt amplifiers (Dixon, 1982) and displayed on a potentiometric flatbed recorder (Smiths, Servoscribe 220, Austria). The essential thermocouple connections are shown in Fig. 3.1. This basic set-up was used in experiments 1 and 3. For experiment 2, the Campbell CR21 datalogger replaced the combined amplifiers and two-pen recorder, and the signals were scanned every 10 s and integrated over periods of 30 minutes. Also, the single thermocouples attached to the leaf were replaced by sets of three parallel sensors, enabling three

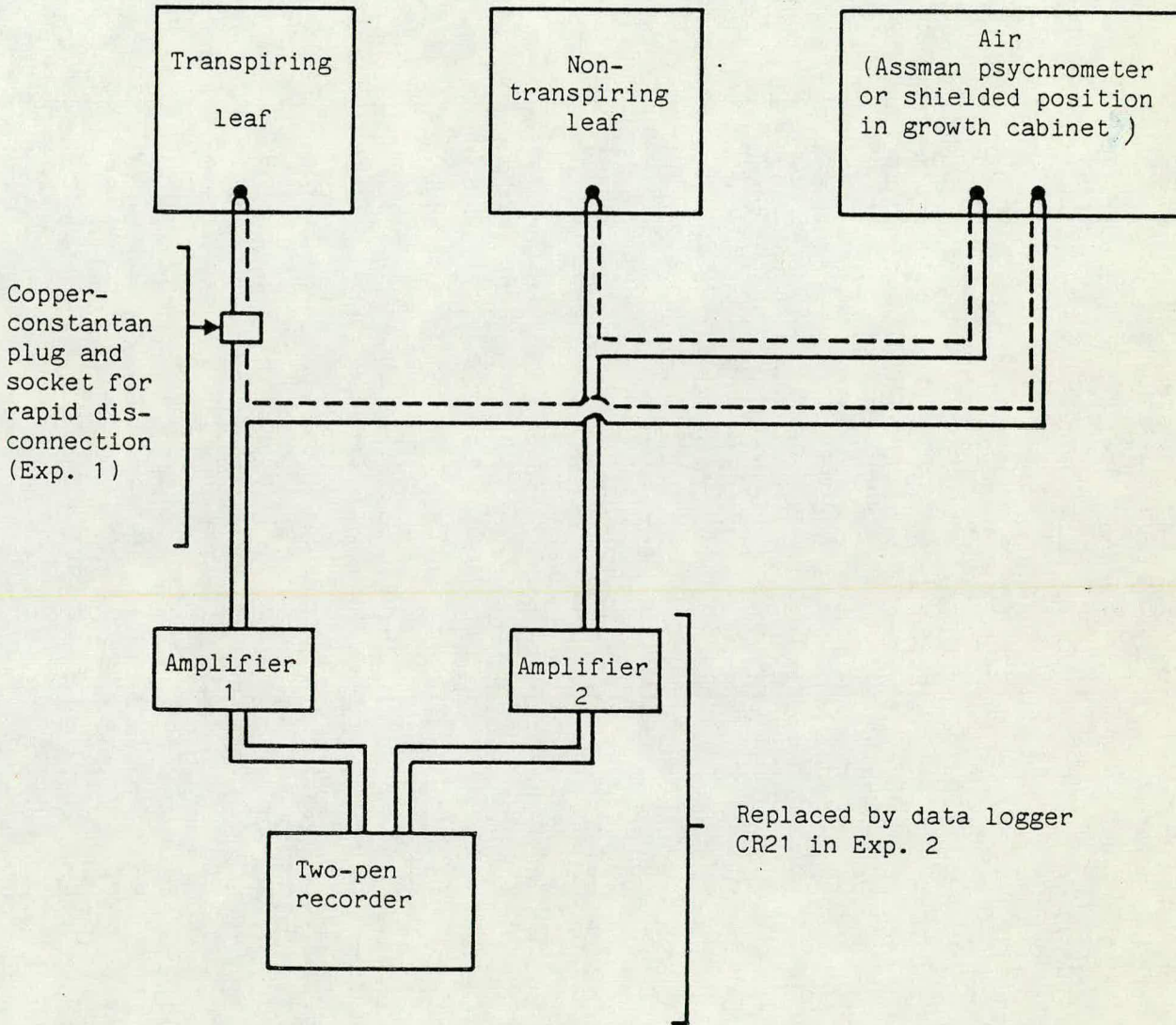


Fig. 3.1 The essential thermocouple connections for the three experiments. Solid line denotes the copper wire, the dashed line denotes the constantan wire.

leaves to be sampled and averaged.

3.1.1 Calibration of the recording system

Thermocouple pairs are subject to three main kinds of errors:

1. If the wires are somewhat dissimilar, a small e.m.f. may be produced even when the junctions are held at the same temperature.
 2. Some batches of wire produce more or less voltage per degree than that normally stated in tables.
 3. The output is only approximately linear with temperature, so that a different calibration should be used for each range of operation.
- In addition, amplifiers are vulnerable to drift in zero and gain on an hourly or daily basis.

All possible precautions were taken to avoid these errors. The thermocouple wires were checked for zero error by immersing the junctions in stirred ice baths. The output of each thermocouple pair was checked by immersing thermocouple junctions in stirred water baths at known temperatures, which were measured with a precision electronic thermometer (Model No. 9535, Guildline Instruments Ltd., Canada), capable of resolving 0.01°C . Typical errors are illustrated in Fig.3.2: at the higher temperatures the thermocouple pair was generally capable of absolute precision to within 0.4°C .

The amplifiers and the chart recorder in experiments 1 and 3 were daily calibrated, to reduce the effect of drift, with a voltage calibrator (D.C. Millivolt Source, Model 404 0.05% Grade, Time Electronics Ltd.), adjusted to give $40\text{ }\mu\text{V}$ to each 1°C .

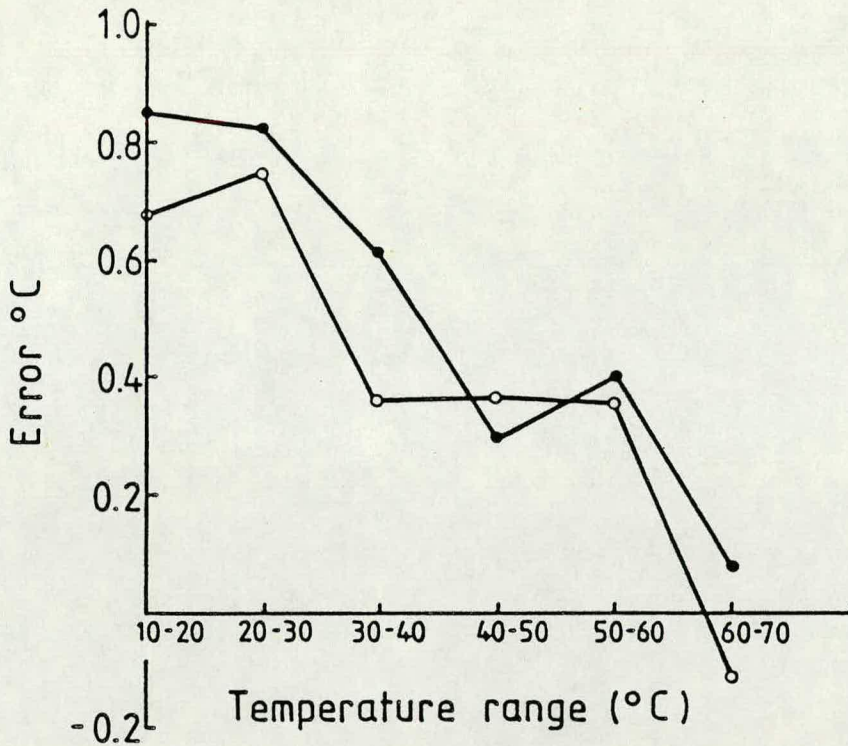


Fig. 3.2

Examples of error in thermocouple signals when pairs were used to sense 10 °C temperature differences between water baths. The baths were set at 10 and 20 °C, 20 and 30 °C, 60 and 70 °C. The actual difference was recorded using the precision electronic thermometer. The temperature sensed by the thermocouple pair was obtained by assuming an ~~out-~~put of $40 \mu\text{V } ^\circ\text{C}^{-1}$. The results apply to actual thermocouples used in experiment 3: ○, those using a transpiring leaf; ●, those used on non-transpiring leaf.

3.1.2 Experimental procedures

3.1.2.1 Experiment 1 - Initial verification experiment

For this purpose two young leaves of a plant were cut off whilst immersed in a water bath. Immediately two plastic tubes (5 ml) were immersed in the water and the petiole of each leaf was inserted into a hole in the lid. This was done under water to prevent entry of air to the xylem. Each tube was sealed with a parafilm tape to ensure no water could be lost except from the leaf.

A thermocouple was attached to each, one of which was vaselined to stop transpiration. The weight of the tube was recorded periodically over the duration of each experiment, which was 3 hours. A sensitive balance (Oertling V20) was used for the weighing (weighing to the nearest 0.0001 g).

Temperature for both leaves, the transpiring and non-transpiring one were recorded continuously over the 30 minute period. The experiment was carried out at three different ambient temperatures: 15, 30 and 40 °C. At the end of each experiment the leaf plan area was determined using a leaf area meter (Li-Cor Model 3100). A new set of the leaves was used in each experiment.

3.1.2.2 Experiment 2 - Later verification experiment

This experiment was carried out in a bigger growth cabinet, aiming once more to compare the transpiration rate which is obtained by the energy balance technique with that obtained gravimetrically. For this purpose 15 potted plants were set out in the Fisons growth cabinet. In the evening prior to the

day of the experiment the plant pots, which had been watered to field capacity, were perfectly sealed with double polythene bags. Five of these 15 plants were chosen randomly to attach the 3 thermocouple sets on 9 of their leaves as described previously, such that 2 sets were sampling 6 transpiring leaves. The experiment ran for two days, at an ambient temperature of 34°C (on the first day) for the comparison with the weighing result, and then at 43°C to study the diurnal trends in g_s of the plant using the energy balance technique with many leaves being sampled simultaneously. The transpiration rate of the entire plant was found by weighing the pots every 3 hours using a pan balance which gives readings to the nearest 0.1g (Sartorius balance). The relative humidity of the room was 35% with a photon flux density of $800 \mu\text{mol m}^{-2}\text{s}^{-1}$.

3.1.2.3 Experiment 3 - Leaf temperature and the evaluation of the boundary layer and the stomatal conductance

For brevity, only one experiment has been reported. However, this experiment was repeated 3 times. It gave similar results always, although it was sometimes spoilt by thermocouples becoming detached. Each time, the temperature of two leaves from two different plants was measured. One of the leaves was allowed to transpire freely while a petroleum jelly (Vaseline) was smeared on the other leaf surfaces to stop transpiration.

The air temperature was raised in daily steps from 30°C

(the temperature at which the plants had been grown) up to 50 °C in intervals of 5 degrees (this will be referred to as the warming phase). Afterwards, the temperature was reduced from 50 to 30 °C in the same steps (the cooling phase). Night temperature was set at 20 °C during the experiment but the saturation vapour pressure deficit (SVPD) was allowed to increase with temperature and was calculated daily by reading the psychrometer in the morning before watering the plants.

3.1.3 Net radiation absorbed by leaves in the growth chambers

It was noticed during the experiments that when the ambient temperature exceeded 40 °C most leaves changed their angles from horizontal to nearly vertical. The vertical position might be expected to reduce the net radiation (R_n) which the leaves absorb. To solve the energy balance, the radiation absorbed at a range of leaf angles was required as the leaf might adopt any angle from horizontal to vertical. For accurate measurements of R_n a Funk net radiometer (type S-1) and a miniature net radiometer (Type ME-1) both manufactured by Swissteco Pty. Ltd., Melbourne, were used for measuring the incoming fluxes of all-wave radiation. A solarimeter (Kipp and Zonen Ltd., Netherlands) was used for measuring the shortwave fluxes.

The incoming fluxes of the long and short wave at various angles were measured by covering the bottom half of the Funk net radiometer with aluminium foil, leaving the upper surface of the radiometer acting as a leaf surface. Then both

the Funk radiometer and the solarimeter were mounted at plant height and orientated at different angles in 15/30 degree steps ranging from 0-180 °C (Fig. 3.3). Therefore at any angle the absorbed energy for a leaf could be calculated as follows:

$$R_n = (AW_d - SW_d) \alpha_l + (SW_d \times \alpha_s) + (AW_u - SW_u) \alpha_l + (SW_u \times \alpha_s)$$

where AW = the all-wave radiation sensed with a radiometer.

SW = the shortwave radiation sensed with a solarimeter.

α_l and α_s are the fractions of the incident energy in the longwave and shortwave bands that are absorbed by the leaf. These must be calculated from a knowledge of the optical properties of the leaf and the spectral energy distribution of the incident radiation. The subscripts d and u denote the downward and the upward components (see Chapter 4, Table 4.3.1)

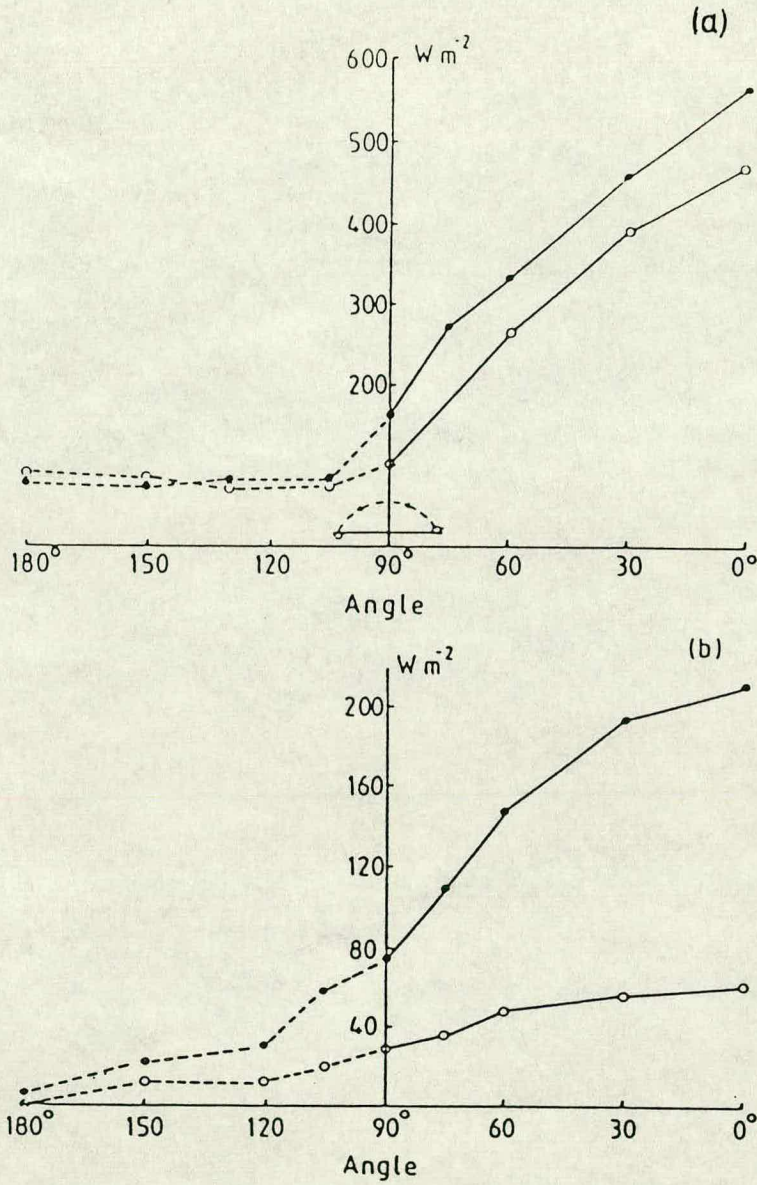


Fig. 3.3 The estimation of radiation absorbed by a leaf in the Fisons cabinet (a) and the Controlled Environment Cabinet (b) at different angles. The angles are measured from the zenith. ●—● = AW_d , ○—○ = SW_d , ●---● = AW_u , ○---○ = SW_u .

3.2 The results

3.2.1 The verification experiments

The calculated transpiration rate E using the energy balance technique is plotted versus the observed transpiration rate E_o (Fig. 3.4). It can be seen that there is a good correlation between E and E_o . The slope of the regression line is 1.05 and the correlation coefficient (r) is 0.95.

Fig. 3.5 shows the pattern of E and E_o during the course of one day (Experiment 2). E was higher than E_o at the beginning of the day but by the middle of the day the two methods showed good agreement. Although E started to decrease before E_o , they became about the same by the end of the day. The daily total transpiration rates $[E]$ and $[E_o]$ were nearly the same. $[E]$ was $7.31 \text{ kg m}^{-2} \text{ day}^{-1}$ whilst $[E_o]$ was $7.53 \text{ kg m}^{-2} \text{ day}^{-1}$.

3.2.2 Leaf temperature and the evaluation of the boundary layer and the stomatal conductance

Leaf temperatures are shown in Fig. 3.6 as a daily average. The non-transpiring leaf was always warmer than the air while the transpiring leaf was slightly higher than that of the ambient temperature when the air temperature was less than 41°C in the warming phase and below 37°C in the cooling phase. At air temperatures higher than 41°C , the leaf temperature was cooler than that of the air. When the air temperature was 50°C the transpiring leaf was 7.5°C cooler than that of the air.

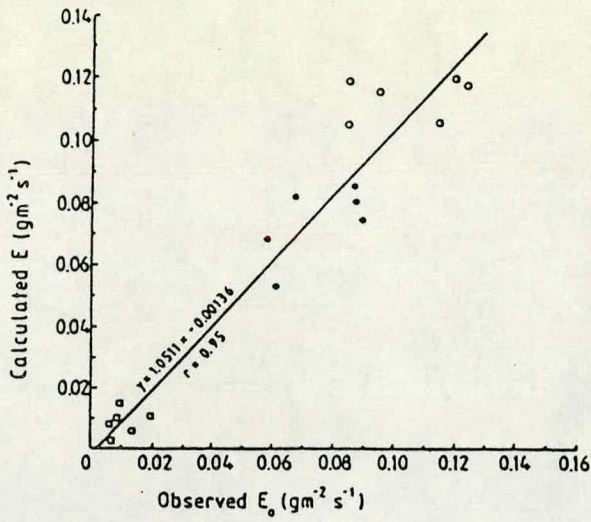


Fig. 3.4 The relationship between the calculated and observed transpiration rate. Data for single leaves of *Citrullus colocynthis* obtained in a controlled environment at three temperatures: ●, 40 °C; ○, 30 °C; □, 15 °C.

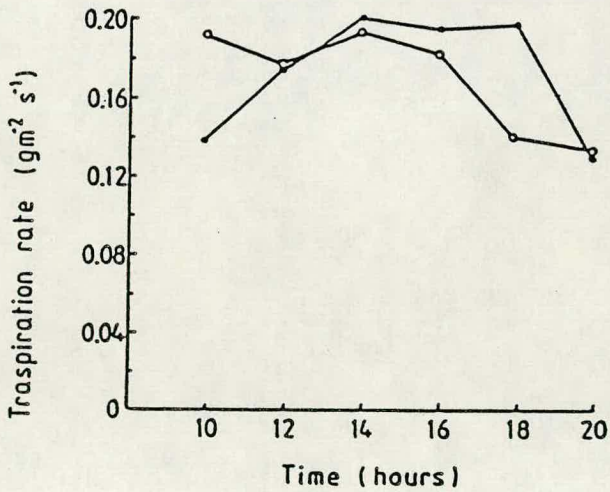


Fig. 3.5 The calculated E (○—○) and the observed E (●—●) as measured simultaneously for a whole day. E values are averaged over 2 hours.

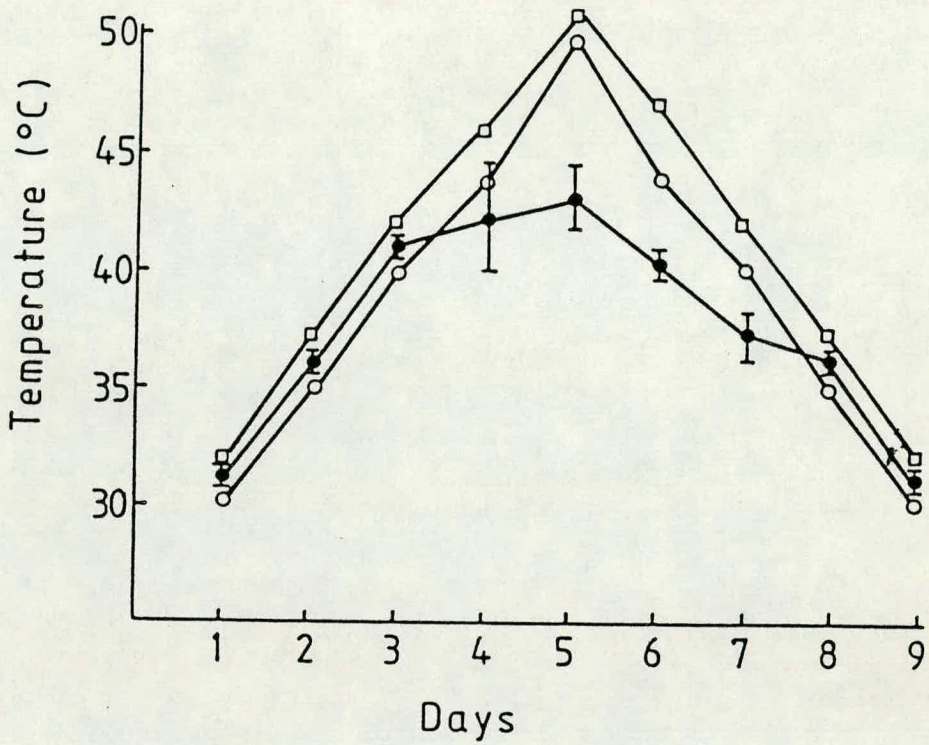


Fig. 3.6

The daily average of the transpiring leaf temperature (●—●) and non-transpiring one (□—□) during the warming and cooling phases. ○—○ is the air temperature. Bars denote the standard errors of a set of 2-hourly readings over the course of each day.

Knowing the leaf temperatures of the transpiring and non-transpiring leaf and applying the leaf energy balance theory as already discussed in the previous chapter, the transpiration rate E and Bowen ratio are shown in Fig. 3.7 with the internal and external resistances that influence the partition of energy. E increased in the warming phase (days 1-5). At an air temperature of 30°C E was less than $0.048 \text{ g m}^{-2} \text{ s}^{-1}$, but it increased up to $0.595 \text{ g m}^{-2} \text{ s}^{-1}$ at an air temperature of 50°C . In the cooling phase E decreased until it reached $0.037 \text{ g m}^{-2} \text{ s}^{-1}$ at an air temperature of 30°C . Part of the increase and subsequent decrease of E were caused by the increase and decrease of SVPD.

Stomatal conductance g_s at air temperatures less than 40°C was below 0.002 m s^{-1} , but as the air temperature was increased above this threshold it started to increase reaching the highest value of 0.015 m s^{-1} at an air temperature of 50°C . In the cooling phase g_s decreased reaching a minimum value of 0.005 m s^{-1} at an air temperature of 35°C . Thereafter g_s was a little higher than the previous day attaining 0.0024 m s^{-1} .

The boundary layer conductance g_a was below 0.091 m s^{-1} at air temperature of less than 45°C ; above this temperature g_a increased reaching its maximum value of 0.178 at an ambient air temperature 50°C . This increase in g_a was surprising as the air flow in the cabinet is constant.

The Bowen ratio (B) is defined as the ratio of the sensible heat flux C to latent heat flux λE (Monteith, 1973). B was positive when the transpiring leaf temperature was above

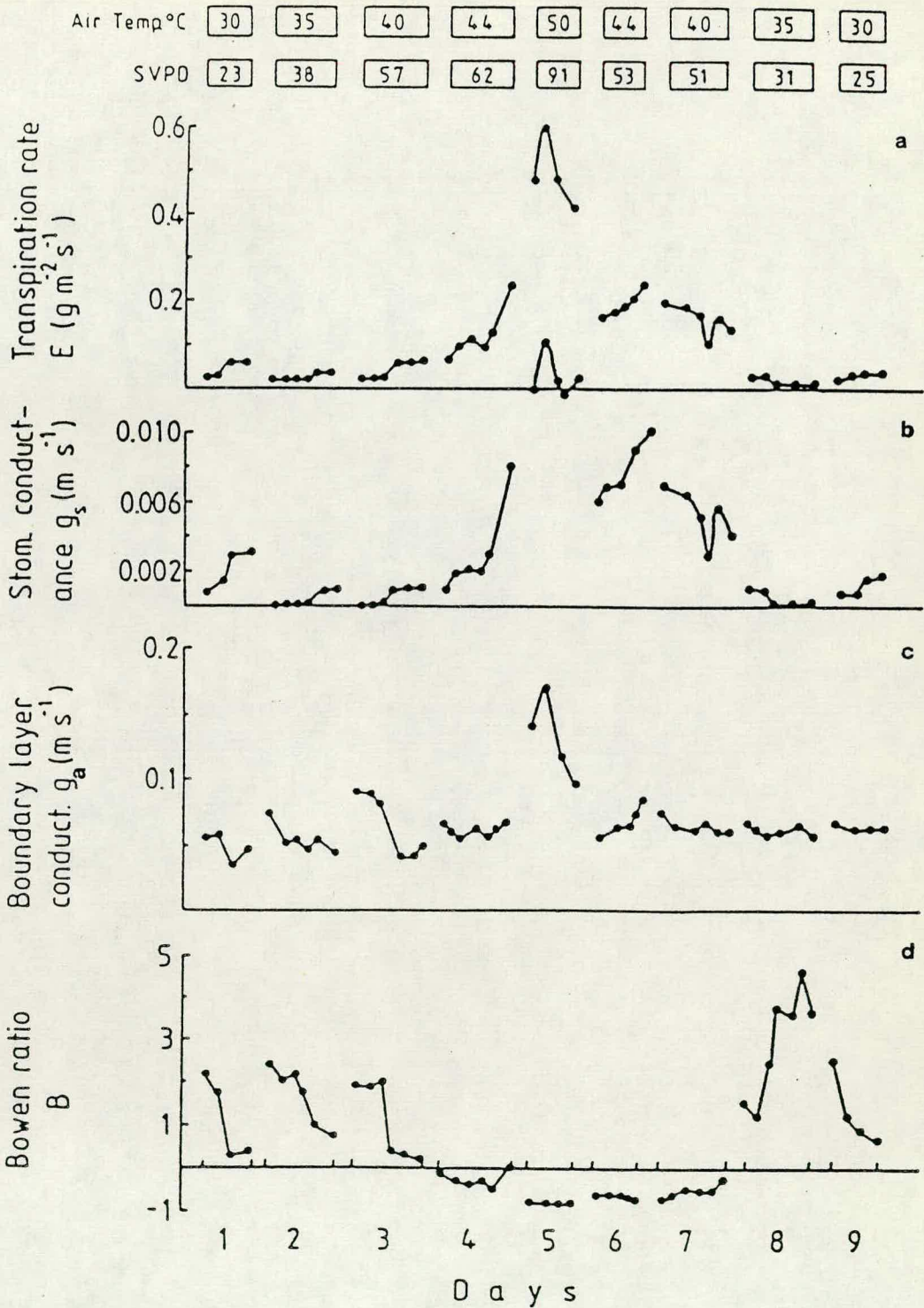


Fig. 3.7

The transpiration rate E (a), stomatal conductance g_s (b), boundary layer conductance g_a (c) and Bowen ratio B (d) during Experiment 3. Most readings were taken every 2 hours. The figure shows air temperature and SVPD during the warming and the cooling phases (boxes).

that of air, but as the transpiring leaf temperature became cooler it decreased to a negative value, the minimum being at the highest air temperature. This is because C changed its sign, being positive when the leaf was warmer than the air, and negative when it became cooler.

Further, more exact information on the diurnal behaviour of E and g_s was obtained by continuing experiment 2 into a second day (Fig. 3.8). E started with a low value ($0.192 \text{ g m}^{-2}\text{s}^{-1}$) in the early morning but as the day progressed it increased to $0.47 \text{ g m}^{-2}\text{s}^{-1}$ at 11.00 hrs. At the end of the day it decreased to $0.138 \text{ g m}^{-2} \text{ s}^{-1}$. A similar pattern was recorded for g_s which was 0.004 m s^{-1} at the beginning of the day reaching a maximum value of 0.015 m s^{-1} at 11.00 hrs and then declining to 0.002 m s^{-1} by the end of the day.

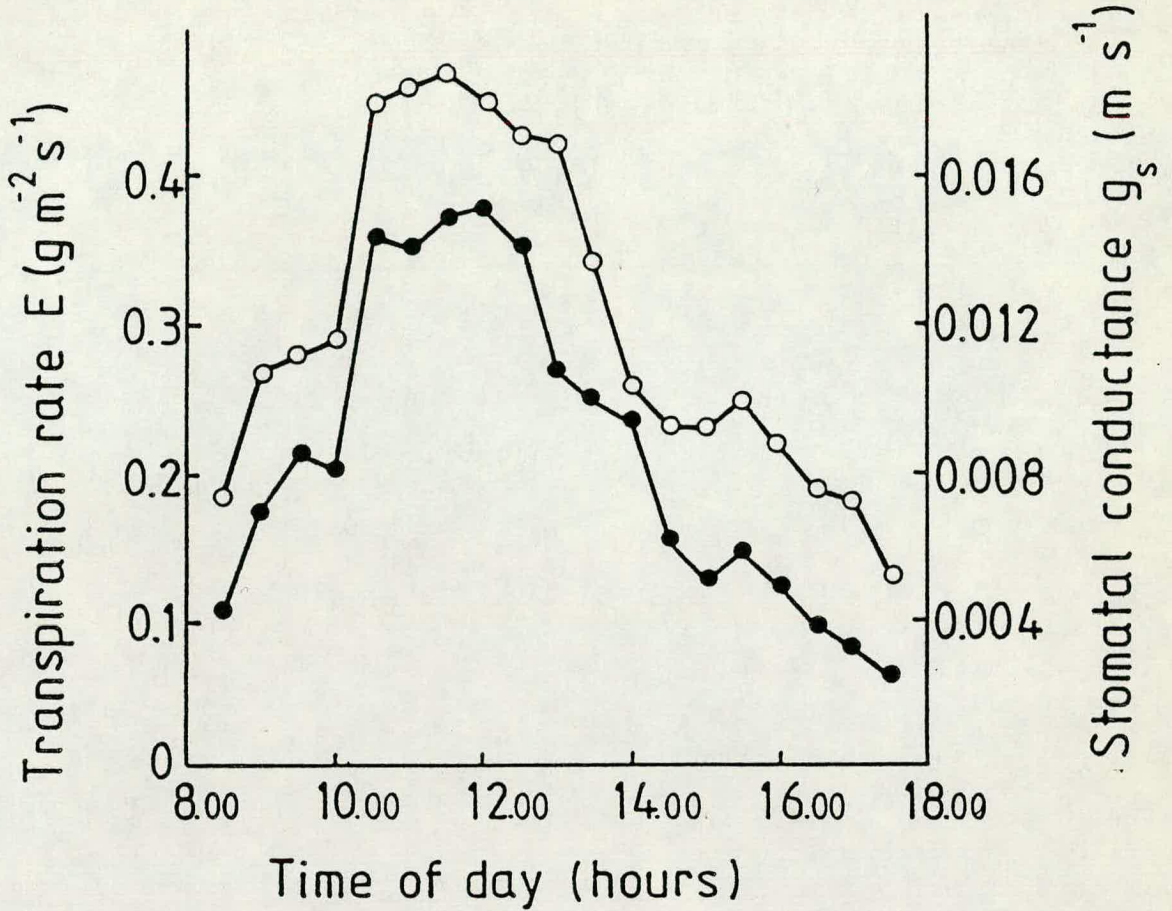


Fig. 3.8

Transpiration rate E (○—○) and stomatal conductance g_s (●—●) of *C. colocynthis*. 6 leaves were sampled at air temperature 43 °C and SVPD 61.4–66.7 (mbar)

3.3 Discussion

The comparisons presented above demonstrate general agreement between the transpiration rate estimated by using the energy balance theory and that observed from weighing. In experiment 1 the relation between E and E_o was clear and of high correlation coefficient. When daily totals of E were compared to those of E_o there was only a small difference between transpiration rates obtained by the two methods. Both comparisons give a confidence in the data obtained by the energy balance technique. However, it is obvious that errors can be encountered with any measuring system. In this case it was thought to be wise to assume that some errors were likely to have occurred during the measurements. These errors could arise during measurement of any parameter including R_n , T_a , T_L and T_L^* . An error analysis was conducted using several calculations in which a standard run was compared with a test run of the calculation. In each test run, the input values were varied to be different from the values assumed in the test run. The parameters in the test run were:

$$R_n = 160 \text{ W m}^2$$

$$T_a = 30 \text{ }^\circ\text{C}$$

$$T_L^* = 31.9 \text{ }^\circ\text{C}$$

$$T_L = 28.5 \text{ }^\circ\text{C}$$

$$\text{WBD} = 10 \text{ }^\circ\text{C} \text{ (WBD is the depression of the wet bulb)}$$

These values were chosen from those that actually occurred in experiment 1. Errors were assumed to be $\pm 15\%$ of R_n and $\pm 0.5 \text{ }^\circ\text{C}$ for the other variables (T_a , T_L and T_L^*). Fig. 3.9 contains

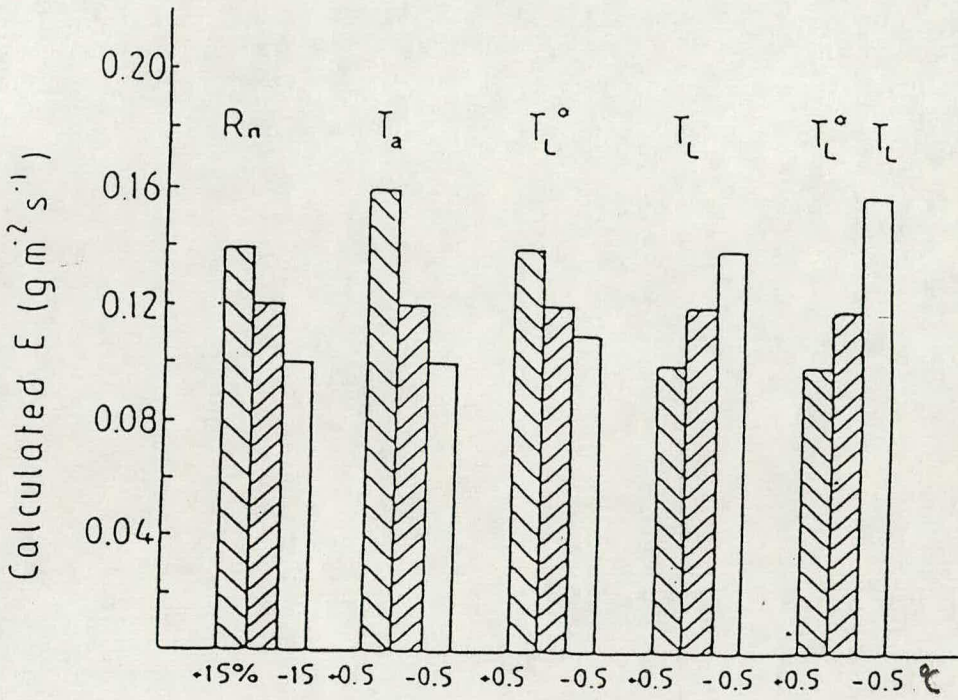


Fig. 3.9

The likely upper and lower limit of errors in the measurement have been assumed, and the calculated result compared to the standard run \square . For specification of the standard run, see the text. R_n the net radiation, T_a air temperature, T_L^* the non-transpiring leaf, T_L the transpiring leaf, $T_L^* T_L$ the non-transpiring and the transpiring leaf temperature.

the original E value beside the recalculation of this value after the assumed errors. It can be seen that an over-estimation of T_a by 0.5°C and an under-estimation of T_L and T_L^* produce the most serious errors by giving an over-estimation of E , although this is unlikely to be encountered with the apparatus used here for measuring the air temperature or by using a fine thermocouple to measure leaf surface temperature. Perhaps the most important source of error in practice results from the use of one thermocouple per leaf; it is known that leaf temperature may vary according to location on the leaf.

To investigate errors in measuring g_s , it was tried several times to use a porometer (Li-1600, Li-Cor, Nebraska) to do the same kind of comparison. Unfortunately, the results obtained by the energy balance technique were always much higher than those obtained by the porometer. This discrepancy might be due to several causes:

1. either the plant stomata are very sensitive to any kind of pressure so they shut as soon as they are clipped inside the porometer chamber due to the pressure caused by the clip or they are very responsive to the light level which is reduced as the leaf is fixed into the chamber.
2. In the porometer chamber the leaf surface is exposed to stirred dry air, therefore the boundary layer adjacent to the leaf would be thinner and stomata might shut due to sudden exposure to the dry air. Normally a leaf is surrounded by a much thicker boundary layer and subsequently, stomata will not be exposed directly to such large VPD values (see e.g. Grace, Malcolm & Bradbury, 1975; Turner, Schulze & Gollang, 1984).

3. The *C. colocynthis* leaf is relatively small and undulating, and it is difficult to achieve a good seal in the porometer chamber.
4. In a controlled environment room, the CO_2 concentrations are inevitably enhanced by the respiration of the worker. Most stomata are sensitive to CO_2 , and perhaps this species is especially sensitive. The response of stomata to the environmental conditions has been discussed by several authors (e.g. Meidner & Mansfield, 1968; Jarvis, 1981; Mansfield, Travis & Jarvis, 1981)

The ability of *C. colocynthis* to lower its temperature as reported by Lange (1959) and Evenari *et al.* (1971) has been confirmed. These later workers recorded a leaf temperature of 7°C below that of the ambient air. The phenomenon is displayed by some other desert plants (Pearcy *et al.*, 1974; Smith, 1978). Other workers reported that when the air temperature exceeds a certain limit the leaves of some species cross over from 'over-temperature' plants to 'under-temperature'. Drake *et al.* (1970) measured leaf temperature of *Xanthium strumarium* in controlled environment: the plant was 'over-temperature' at an air temperature below 35°C . Above that the plant became an 'under-temperature'. Gates (1976) reported the same phenomenon for plants growing in a controlled environment. *C. colocynthis* leaves exhibited the same phenomenon as already mentioned in the results section.

Applying a knowledge of T_L and T_L^* to solve the leaf energy balance and calculating the partitioning of the energy absorbed (E and C) leads to the conclusion that *C. colocynthis* displays very high transpiration rates and dissipates most of

the incident energy in this way. This is a consequence of an especially high g_s and a fairly high g_a . E increased with T_a over the period when SVPD was increasing. Drake *et al.* (1970) in their work on *Xanthium* leaves found that leaf conductance increased with increasing T_a . Other workers such as Schulze *et al.* (1973) reported that when the plant was not under water stress the diffusion resistance for water vapour decreased with increasing air temperature, and the stomata remained fully open (Gates, 1980). The relation between the transpiration rate and stomatal conductance on one hand and the stomatal conductance and air temperature on the other hand is a question which has been a subject of much discussion in recent years. Some workers have found that g_s decreases with increasing VPD whereas others found that stomata shut at low VPD (Meidner & Mansfield, 1968;; Gates, 1980; Osonubi & Davies, 1980; Jarvis & Morison, 1981).

From the present work leaf conductance of *C. colocynthis* can apparently be as high as 0.015 m s^{-1} . Comparing that with values of g_s of other species (see e.g. Smith, 1978; Körner, Scheel & Bauer, 1979) we find the plant has a high stomatal conductance among desert species particularly at high air temperatures.

The aerodynamic conductance g_a was low at low air temperature and low transpiration rates but at high T_a it increased. However the air flow in the room was constant and the only obvious change occurring to the leaves was in their posture: they moved to a nearly vertical posture at $T_a > 40^\circ \text{C}$. The effect of leaf posture on g_a will be discussed in Chapter

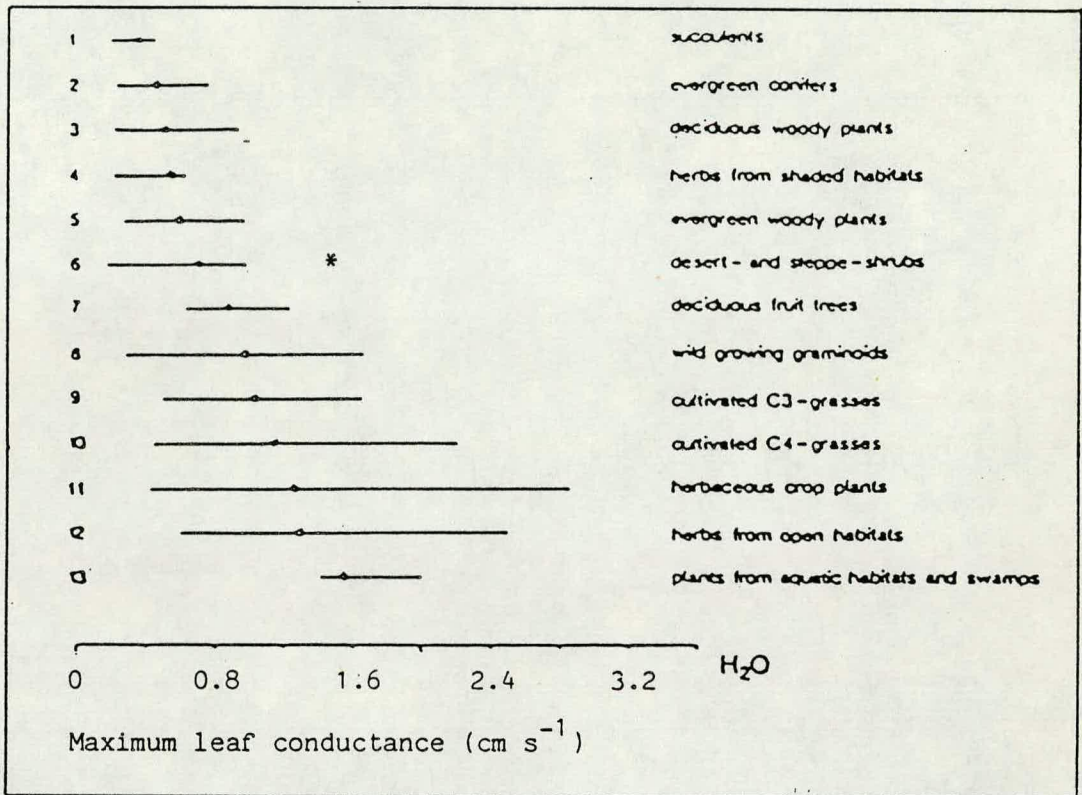


Fig. 3.10 Stomatal conductance of *C. colocynthis* (*) compared with other species. Values have been corrected to a plan area basis (reproduced after Körner et al., 1979).

4. This might cause more turbulence and enhance the heat transfer from the leaf (Grace, Fasehun & Dixon, 1980; Grace, 1983). More likely, the effect is simply due to the increased air flow close to the leaf as it adjusts from a sheltered posture close to a more exposed posture when held aloft.

CHAPTER 4
PHYSICAL ATTRIBUTES OF
C. COLOCYNTHIS LEAVES

4.1 Introduction

In the field study it was noticed that some leaves were held nearly vertical while others on the same plant exhibited a nearly horizontal posture. This phenomenon was again observed in experiments which were carried out in the controlled environment growth cabinets in Edinburgh. Therefore the estimation of the effect of the leaf posture on the boundary layer resistance (or conductance) was thought to be necessary for two reasons. Firstly to determine whether the vertical position of the leaves has any functional value in promoting heat loss from the leaves. The second reason pertains to the application of the energy balance technique outlined in Chapter 2. In the calculations, the boundary layer resistance r_a of the non-transpiring leaf is required to facilitate calculation of the energy balance of the transpiring leaf, and in doing so the assumption is made that both leaves have the same posture and thus the same r_a . If this is not the case, special provision must be made to calculate r_a of the transpiring leaf. This will be covered in the first part of this chapter. The second part will address another problem involved in the matching of leaves. It is important to establish whether the transpiring and non-transpiring leaves exhibit identical optical properties. Once more, if they are

different, it is important to know the extent of the difference in order to make a correction in the calculations of the energy balance.

4.2 Leaf boundary layer conductance determination

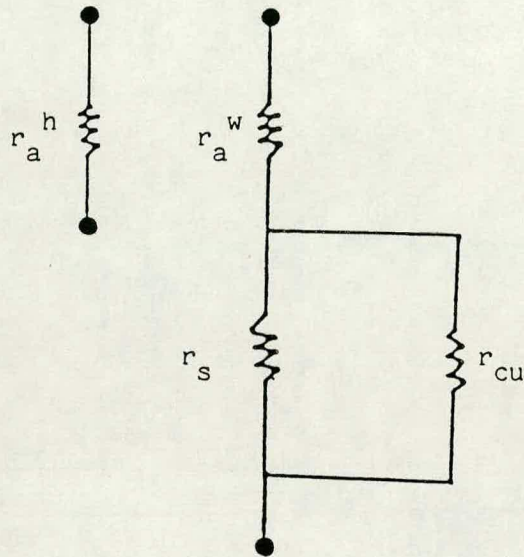
4.2.1 Background

When air flows along a surface it tends to stick to that surface and hence its velocity decreases, being zero at the surface and increasing with distance measured perpendicular to the surface. The region of reduced velocity is known as the boundary layer, and varies in thickness according to the distance from the leading edge, measured parallel to the surface (Grace, 1977; Gates, 1980). Heat and mass exchange between a leaf and the surrounding air takes place across this layer. The exchange rate is determined broadly speaking by the average thickness of the boundary layer and the driving gradient. The boundary layer thickness depends on several factors such as the surface roughness, its shape, the wind speed and to a smaller extent, its orientation (Vogel, 1970; Oke, 1978; Grace, Fasehun & Dixon, 1980).

The mass exchange through the boundary layer is driven by the concentration gradient between the surface and the surroundings according to Fick's law of diffusion. However, heat loss from a plant leaf is governed by the temperature gradient between the leaf surface and ambient air. The rate of the heat loss is determined by the boundary layer resistance r_a while in the case of the water vapour exchange there is an

additional resistance due to the length of the diffusion path through the stomatal pores including their substomatal cavities.

For simplicity, and as a visual aid, some workers prefer to represent the resistance to the diffusion pathway as an electrical analogue first proposed by Gaastra (1959).



where r_a^h = the boundary layer resistance to heat transfer
 r_a^w = the boundary layer resistance to water vapour transfer
 r_s = the stomatal resistance
 r_{cu} = the cuticular resistance

Because r_{cu} usually is so large, any fluxes of water vapour through it is ignored except in certain cases.

Note that resistance can be simply defined by analogy to Ohm's law for electrical flow:

Ohm's law:

$$\text{resistance} = \frac{\text{voltage difference}}{\text{current}}$$

Fick's law of diffusion:

$$\text{resistance} = \frac{\text{concentration difference}}{\text{flow}}$$

Irrespective of whether we consider mass diffusion (as for H_2O or CO_2), or heat diffusion (convection) the units of resistance are always the same:

for mass

$$r = \frac{\text{kg m}^{-3}}{\text{kg m}^{-2} \text{ s}^{-1}} = \text{s m}^{-1} \quad (4.1)$$

For heat, remembering that a difference in heat content can be obtained from a temperature difference ΔT by multiplying it by ρC_p (ρ is the density of the medium and C_p is the specific heat). C is the flow of heat:

$$r = \frac{\rho C_p \Delta T}{C} = \frac{(\text{kg m}^{-3}) (\text{J kg}^{-1} \text{ } ^\circ\text{C}^{-1}) ^\circ\text{C}}{\text{J m}^{-2} \text{ s}^{-1}} = \text{s m}^{-1} \quad (4.2)$$

Resistances for different entities (heat, H_2O , CO_2) are related to each other if they share an identical diffusion path. For purely molecular diffusion through a tube (like a stomatal pore) the corresponding resistance r^h , r^{H_2O} , r^{CO_2} may be inter-related through the diffusion coefficients of heat, water and CO_2

$$\frac{r^x}{r^y} = \frac{D^y}{D^x} \quad (4.3)$$

where the superscripts x and y refer to the entities and D^y and D^x are corresponding diffusivities. However, rather more complex inter-relationships occur for diffusion through boundary layers (Grace, 1981) :

$$\frac{r^x}{r^y} = \left(\frac{D^y}{D^x} \right)^{0.66} \quad (4.4)$$

Some authors prefer to use the reciprocal of r_a , the boundary layer conductance g_a , as the transfer rate is directly proportional to the conductance. In older literature the heat transfer coefficient h_c is used, where the relationship between g_a and h_c is as follows:

$$h_c = \frac{C}{T_L - T_a} \quad (4.5)$$

where h_c = the heat transfer coefficient ($J \, m^{-2} s^{-1} \, ^\circ C^{-1}$)

C = the convection heat flux density at the leaf surface (Wm^{-2})

T_L = the temperature of the leaf surface ($^{\circ}\text{C}$)

T_a = the temperature of the ambient air ($^{\circ}\text{C}$)

The boundary layer conductance g_a for the same leaf can be defined as

$$g_a = \frac{C}{\rho \text{ Cp } (T_L - T_a)} \quad (4.6)$$

where ρ = the density of air (kg m^{-3})

Cp = the specific heat of air at constant pressure ($\text{Jkg}^{-1}\text{C}^{-1}$)

by comparing equations (4.5) and (4.6) the heat transfer coefficient h_c is :

$$h_c = \rho \text{ Cp } g_a \quad (4.7)$$

4.2.2 Technical evaluation

Several techniques have been used for measuring the boundary layer resistance r_a to heat and water vapour from plant leaves. The most common technique which has been used until recent years employs a filter paper replica of a leaf which is saturated with water. The evaporation rate of the water vapour from the leaf replica is measured. For leaves of conifers, a coating of calcium sulphate serves to hold water in a variation of this method reported by Landsberg and Ludlow (1970). In this method several measurements are required: weighing the model before and after the evaporation process takes place, measuring the temperature of the evaporating surface and determining the water vapour pressure of the air in the room (Gaastra, 1959; Thom, 1968; Jarvis, 1971; Grace & Wilson, 1976). Disadvantages of this method arise from the difficulty in knowing precisely the surface temperature because of the evaporation continuously occurring during the weighing period and knowing accurately the vapour pressure of the air. Grace and Wilson (1976) discussed the errors associated with this technique such as the difficulty in estimating the model surface-air VPD and the model manipulation during the weighing process. Other workers have applied substances such as naphthalene to the replica surface. This material sublimates with negligible cooling and the rate can be found by weighing (Sherwood & Bryant, jr, 1957; Neal, 1975). By applying the naphthalene to the model surface under investigation, the difference in the model weight before and



after treatment due to subliming of the naphthalene could be measured. The disadvantages of this method is the difficulty in knowing the naphthalene concentration which eventually builds up in the room where the experiment is taking place and the difficulty in spraying the naphthalene evenly to the surface. For the same purpose other researchers used the electrochemical method in which the convective transfer of ions to the leaf replica, acting as a cathode, placed in an aqueous solution can be recorded (Schnepp, 1972; 1973). The disadvantage of this method is that it is so far removed from the natural process that conversion of the results to apply to the field situation is of doubtful relevance.

4.2.3 The cooling curve technique

Due to the difficulty in obtaining good measurements of the boundary layer resistance to water vapour r_a^w , it was found better to measure the boundary layer conductance g_a for brass leaf replicas by using the cooling curve technique (Grace, Fasehun & Dixon, 1980; Jones, 1983).

Grace *et al* (1980) calculated g_a of brass leaf replicas as follows:

$$g_a = \frac{bwm}{\rho C p \Delta T} \quad (4.8)$$

where b = the specific heat of brass ($370 \text{ J kg}^{-1} \text{ } ^\circ\text{C}^{-1}$)

w = the brass leaf weight (kg)

m = the slope of the regression line of the logarithm (\ln) of

the replica-air temperature difference ($^{\circ}\text{C}$) on time (s), i.e.

the rate of fall in temperature (s^{-1})

ρ = the density of air (kg m^{-3})

C_p = the specific heat of air ($1010 \text{ J kg}^{-1} ^{\circ}\text{C}^{-1}$)

A = the plan area of the brass leaf (m^2)

note: at this stage we are using plan area and thus following the normal convention in plant science.

It is also possible to estimate g_a from formulae given in books of heat engineering. As the conductance is proportional to the square root of the wind speed and inversely proportional to the square root of the leaf dimension d , the boundary layer conductance can be found as follows:

$$g''_a = \frac{0.66 D^{0.67} u^{0.5}}{d^{0.5} \nu^{0.17}} \quad (4.9)$$

where D = the thermal diffusivity of dry air ($0.21 \text{ m}^2 \text{ s}^{-1}$)

u = the wind speed (m s^{-1})

ν = the viscosity of dry air ($0.15 \text{ m}^2 \text{ s}^{-1}$)

d = the characteristic dimension of the leaf replica (m)

the double prime " is used to show that this formulae applies only when all the surface from which heat is being lost is taken into account.

Thus, if the object is a leaf, both upper and lower surfaces (i.e. twice the plan area) must be used to obtain the conductance.

4.2.3.1 Materials and methods

Two leaf replicas of brass sheet (0.2 mm thick) were made and their margins were carefully shaped to represent juvenile and mature *C. colocynthis* leaves. The models were polished to reduce their emissivity thus reducing radiative dissipation, making it practically negligible (Dixon, 1982).

A set of three 0.1 mm diameter thermocouple junctions (42 SWG) connected in parallel was used for each leaf replica. The set was attached to the abaxial surface of the leaf replica to sense the brass leaf temperature. Sellotape glue was used for attaching the thermocouple junctions to the model, and the film of glue on the junctions isolated them electrically from the brass. The surface temperatures were sampled in 3 positions as shown in Fig. 4.2.1. The reference junction was mounted in the air slightly above and next to the brass leaf. A small piece of putty (Blue Tac) was used to encase the reference junction to reduce its response time and thus suppress unwanted 'noise'. The thermocouple output was amplified using a DC Microvoltmeter (Dixon, 1982). The signals were displayed using potentiometric flatbed recorders (Smiths, Servoscribe, Austria; and Bryons Southern Instruments Ltd., Model 28000, Surrey). The experiment was conducted in two controlled environments: in the Fisons growth cabinet (see chapter 3 for the cabinet description) to measure g_a at different leaf orientations and in the wind tunnel (Department of Forestry and Natural Resources, Edinburgh University) to

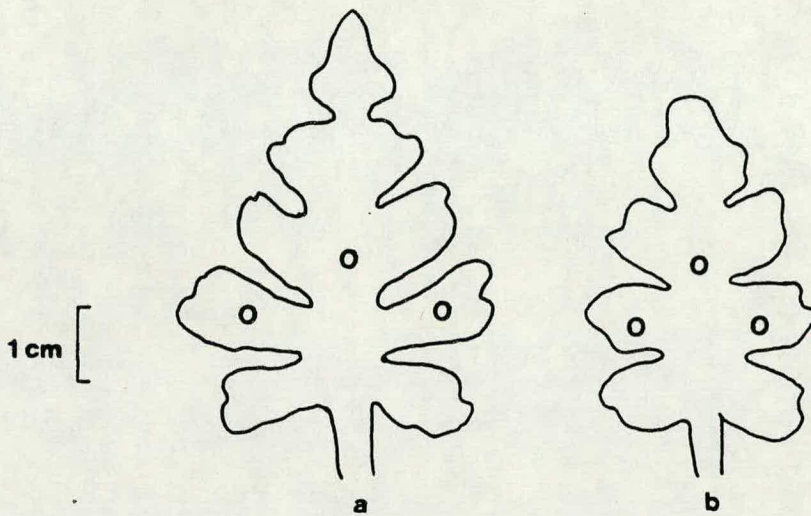


Fig. 4.2.1 Outline of the brass replicas of *C. colocynthis*. The circles show the position of the thermocouple junctions on the leaf, (a) represent the mature leaf and (b) a young leaf. Only the model (a) was used for determining the boundary layer conductance at different leaf postures.

determine the leaf boundary layer conductance g_s at different wind speeds. To obtain low wind speed ($< 2 \text{ m s}^{-1}$) a screen of woven fabric was fixed in the throat of the wind tunnel. The wind tunnel was calibrated by using a pitot-static tube. The brass leaves were held by small wooden clips, as wood is a very poor conductor of heat, and placed in the centre of the controlled environments. Experiments were carried out in the dark to eliminate any radiation coupling. The lights were switched off a few hours before each experiment ran to ensure isothermal conditions. A hair drier was used to heat the upper surface of the brass leaf.

When the leaf replica became $8-10^\circ\text{C}$ warmer than the air temperature the heater was quickly taken out of the cabinet to prevent further radiative exchange and the door was closed. When the leaf replica temperature decreased to about 5°C above the air, the chart recorder was turned on at a known speed. The brass leaf temperature was found to fall exponentially with time, eventually reaching ambient air temperature. The slopes of linearized cooling curves m in equation 4.8 were calculated. Determinations were done for an isolated leaf, held away from the walls, and also on a leaf which was attached to the plant and thus influenced by the aerodynamic properties of the neighbouring leaves. This later situation, henceforth referred to as 'within the canopy', is illustrated in Plate 4.1.

The characteristic dimension d of *C. colocynthis* leaf was determined as described by Grace et al (1980) for determining a lobed leaf by drawing parallel chords on the leaf outlines at

intervals of 0.5 cm. The total of all chord lengths was divided by the number of chords to find d by the mean-of-total-chord method. That was done to the leaf outline in two directions; the long leaf dimension d_l and short leaf dimension d_s .



Plate 4.1 The brass leaf replicas (a & b) standing within *C. colocynthis* canopy.

4.2.4 The results

The effect of leaf angle on the boundary layer conductance g_a of isolated models is shown in Fig. 4.2.2. The effect, if any, was small. When the leaf replica was mounted within the plant canopy the boundary layer conductance g_a was increasing with the leaf angle. Maximum g_a was found at a leaf angle of 90° .

Fig. 4.2.3 shows the boundary layer conductance g_a for *C. colocynthis* models at different wind speeds and two leaf postures. Values of g_a for the mature leaf replicas are plotted in (a) and for the juvenile model in (b). Maximum boundary layer conductance g_a was found when the isolated leaf replica was standing vertically for both leaf models, the mature and the juvenile. The lowest conductances were measured for leaf replicas when they were standing at angle 30° , and the highest when they were standing vertically within the canopy. At low wind speed ($< 2.5 \text{ m s}^{-1}$) g_a values for both leaf models were very similar irrespective of their positions.

A comparison between the observed and calculated boundary layer conductance g_a'' are shown in Fig. 4.2.4. It is noteworthy that whereas the magnitudes of g_a'' are in broad agreement there is a systematic departure between the shapes of the observed and calculated relationships. This is especially noticeable in the case of the mature leaf replica, where the measured conductances at low wind speeds are less than expected whereas at high wind speeds they exceed the expected values.

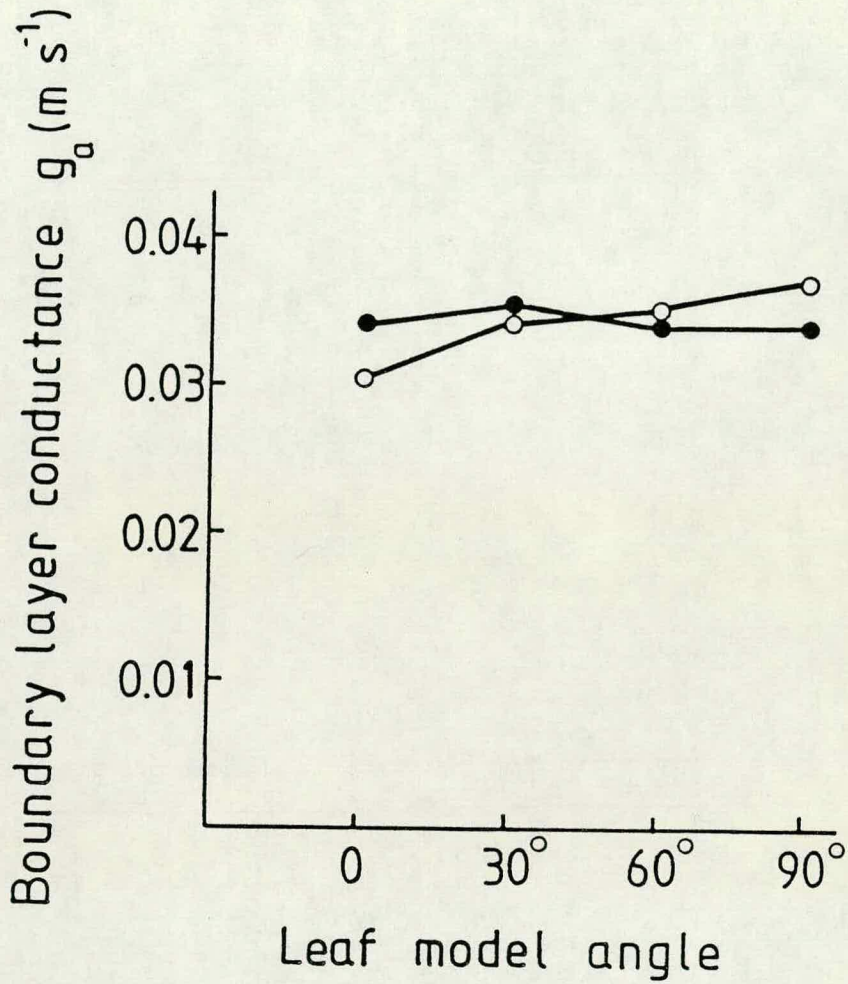


Fig. 4.2.2 Boundary layer conductance of *C. colocynthis* replica (for a mature leaf) at different orientations. Open circles for a model within the plant canopy and solid circles for an isolated leaf replica. Each point is an average of 3 cooling curve determinations. The experiment was carried out in the controlled environment room where the wind speed is about 0.5 m s^{-1} .

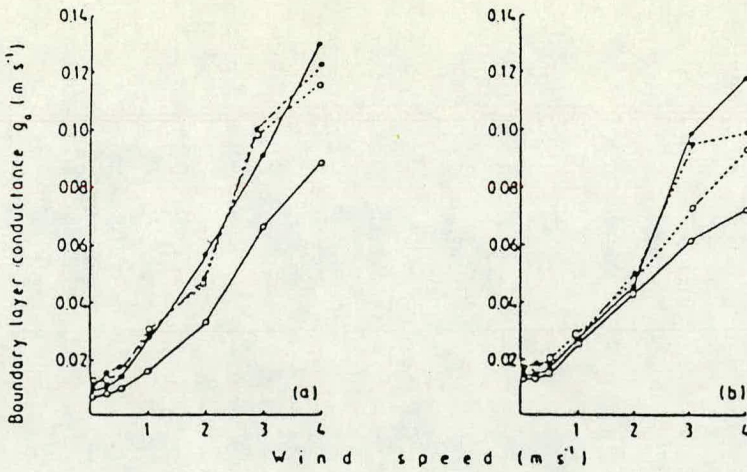


Fig. 4.2.3 The boundary layer conductance for a leaf model at an angle of 30° (solid line) and at an angle of 90° (dashed line). Solid circles represent isolated leaf replicas and open circles denote models standing within the canopy. (a) a mature leaf replica, (b) juvenile leaf model.

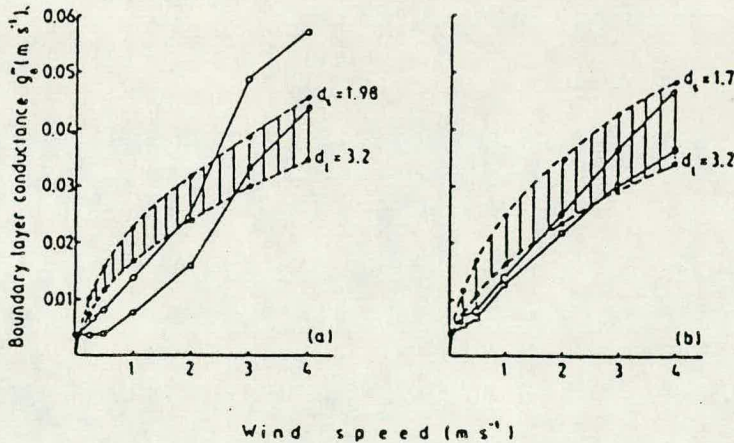


Fig. 4.2.4 The comparison between the observed and the calculated boundary layer conductances in the canopy. The shaded areas are values of calculated conductances, the solid circles denote leaf dimension d_s and the solid squares represent d_L (see the text). Both surfaces of the leaf were combined together to determine the boundary layer conductance g''_a . Open circles denote a leaf model standing vertically within the canopy. The open squares represent the calculated g''_a for a leaf of 30° . (a) conductance for a mature leaf and (b) for a juvenile one.

4.3 Leaf optical properties

4.3.1 Background and literature review

Optical properties of plants vary among species according to several factors. Some of these factors are internal such as the structure and thickness of the leaves whilst others are external such as surface composition or the presence of a pubescent layer as found in many of the arid zones plants (Ross, 1975; Gates, 1980). In general most leaves absorb 75-90% of the visible light (400-700 nm wavelength) this waveband being coincident with that utilized in the photosynthetic process. In the near infra-red waveband (700-1200 nm) leaf absorptance decreases remarkably but beyond this region the radiation absorption increases and plant leaves behave as black bodies by absorbing all the incident radiation acting as practically perfect radiators (Monteith, 1973; Gates, 1980; Nobel, 1983).

Desert plants which are exposed to a high load of radiation for most of the day must have some adaptive characteristics to minimize absorption of solar radiation. Some authors pointed out that the light green or greyish appearance of desert leaves is of importance, suggesting a high reflectance (Daubenmire, 1974). In addition, pubescence is thought to be of much value in decreasing absorptance. Billings and Morris (1951) reported that pubescence increased the reflectance in the visible light of the solar radiation but they do not have that effect in reflecting the infra-red waveband. However, there is no consensus on the role of pubescence concerning the spectral reflectance. Some authors

reported that although hairs increase reflectance in the visible part of the spectrum, they do not change the total energy absorbed by the leaves. Others found that pubescence increases the reflectance of the near infra-red wavebands and they do not effect longer wavelength. Further discussion of thorns and pubescence is available in Gates (1980).

It is clear that plants display different optical properties, according to their habitat and this property may vary with season. Billings and Morris (1951) found that the greater the exposure to the sunshine and the drier the habitat, the greater was the leaf reflectance in the visible spectrum. At 550 nm desert plant species had an average reflectance of 26.6% while the shaded, irrigated species had a reflectance of 13.6%. In dry periods, there is an evident need for the arid zone plants to undergo a decrease in absorptance to solar radiation . In an investigation on three desert plants, the absorptance decreased from 0.61 in the wet season to 0.43 in the dry season by increasing the pubescence on the leaves (Smith & Nobel, 1977a). Other workers reported the same phenomenon in other desert plants (see e.g. Ehleringer, 1980; Gates, 1980).

Generally desert plants have a high reflectivity to the solar radiation. *Welwitschia mirabilis* which has a thick, leathery leaf reflected 38% and absorbed 56% of global radiation (Schulze et al, 1980). Gates (1980) reported much higher reflectance of the succulent desert plant *Agave americana* which at 800 nm reflected 80% of the incident radiation.

The optical properties of the leaf are required in the

estimation of the net radiation R_n that the leaf absorbs in the field, from a knowledge of short wave and long wave fluxes. Moreover, in the energy balance technique which is used in the present study (Chapter 2), optical matching of transpiring and non-transpiring leaves is desirable. Otherwise, calculations require as input data the two values of R_n , corresponding to transpiring and non-transpiring leaves.

Some authors have tried to investigate the influence of the petroleum jelly (vaseline), which often is used as a coating substance to prevent transpiration, on the optical properties of the leaf. Thorpe and Butler (1977) measured the shortwave absorption of an untreated leaf and a vaselined one. The absorption of the two leaves showed no significant difference between the intact leaf and the treated one. The optical properties of a *C. colocynthis* intact and vaselined leaf are reported here, along with those of a cardboard replica as used in the field in one of the main parts of this work (Chapter 8).

4.3.2 Material and equipments

For measuring the optical properties of the plant, healthy fully expanded leaves from potted plants which were grown in a Fisons growth cabinet for 6 weeks were chosen. Measurements were also made on cardboard models of *C. colocynthis* which were cut from cardboard sheet 1.0 mm thick and painted with green paint to resemble, as closely as is possible to detect with the human eye, the colour of the real leaves.

The reflectance and transmittance of intact leaves was measured, and each time the vaseline was applied afterwards to the same leaf and then it was remeasured. Reflectance and transmittance were measured on the upper surface of the plant leaves, in the waveband 400 to 1100 nm using two scanning spectroradiometers. The first of these was the demonstration model of the Li-cor LI 1800 brought to the Department for one day by Mr. Larry Mittendorf, the Director of Li-Cor. The second of these was the same model in Professor Monteith's Department at Nottingham University. However, the latter, for reasons of economy, was fitted, not with the Li-Cor integrating sphere, but with one made by Macam, Livingston, Scotland.

The absorption a for the intact leaf, the vaselined one and the cardboard model was defined as follows:

$$a = \int_{\lambda=400}^{\lambda=1100} (F \cdot (1 - (r + t))) d\lambda$$

where F = the flux density of the spectral energy from the lamps in the growth room or the sky in the field (Appendix B).
 r = the reflectance measured in the integrating sphere
 t = the transmittance measured in the integrating sphere
 λ = wavelength.

The integration was done numerically using a step length of 20 nm. As well as calculating the overall absorptance, the short wave (400-700) nm and near infra-red absorptances were calculated separately.

When working with the second instrument it was noticed

that the reflectance and transmittance curves for the leaves were incorrect as at the longer wavelength their sum exceeded 1.0.

This was also evident when comparison was made with results obtained with the first instrument. Therefore correction factors were calculated and applied to the result from the second instrument, on the assumption that the plant material examined using the two instruments was essentially the same and that the first instrument was correct (the integrating sphere on the Nottingham instrument has since been returned to it's makers for modification). At the time of doing this work, no other spectroradiometer with integrating sphere and suitable waveband range could be located in the United Kingdom.

4.3.3 The results

Table 4.3.1 shows the absorption of unvaselined and vaselined leaf of the *C. colocynthis*. The absorption of the shortwave solar radiation differs only a little, but in the near infra-red part of the spectrum the vaselined leaf had a higher absorption. The unvaselined leaf had practically the same shortwave absorption in all environments whilst the vaselined leaf had somewhat but not drastically different absorptions in all three environments.

The reflection of the intact, vaselined leaf and the cardboard leaf model are shown in Fig. 4.3.1. It can be seen that the unvaselined and the vaselined leaves are very similar at all the measured wavelengths (400-1100 nm) while the model reflects less than both of them except at 500 nm and 1000 nm where it reflects more.

The overall spectral properties of the unvaselined leaf, vaselined leaf and the cardboard model are shown in Fig. 4.3.2 over the waveband 400-1100 nm.

	Controlled environment growth cabinet		Fisons cabinet		Solar global radiation	
	Shortwave	Near IR	Shortwave	Near IR	Shortwave	Near IR
The plant intact leaf	0.81	0.12	0.81	0.12	0.82	0.12
Vaselined leaf	0.78	0.43	0.80	0.54	0.83	0.56
Cardboard leaf model					0.89	0.81

TABLE 4.3.1: The absorption of the incident radiation, at shortwave (400-700 nm) and near IR (700-1100 nm) for the intact leaf, vaselined leaf and a cardboard leaf model. See Appendix B for the spectral energy in each environment.

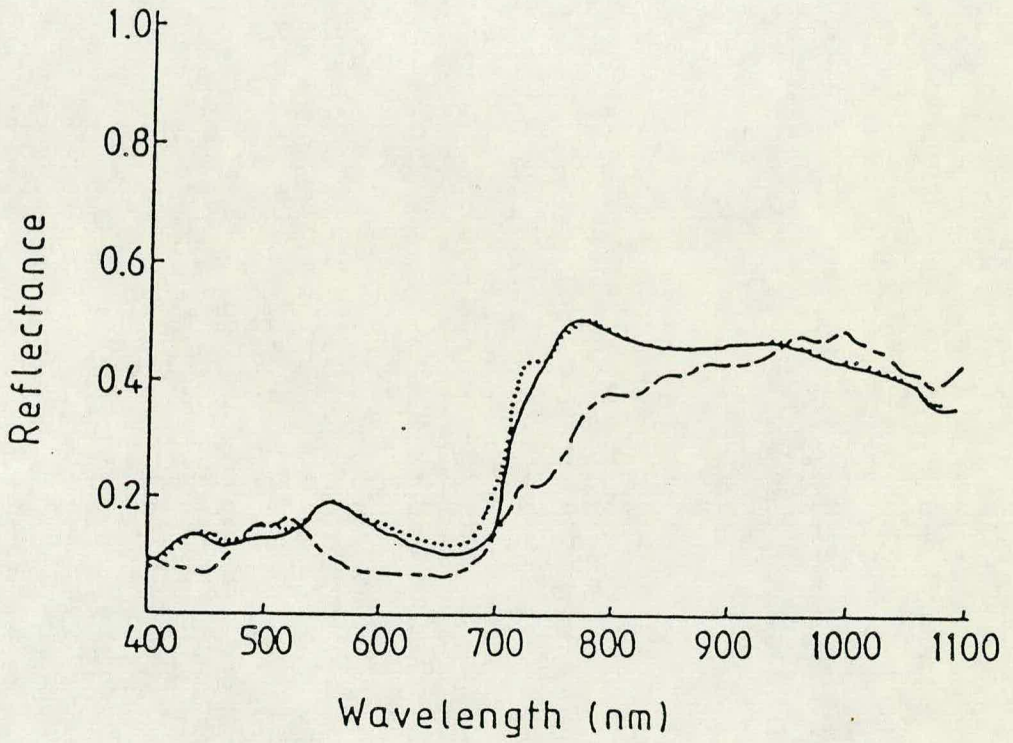


Fig. 4.3.1 The reflectance of the *C. colocynthis* intact leaf (—), vaselined leaf (.....) and the cardboard model (—•—).

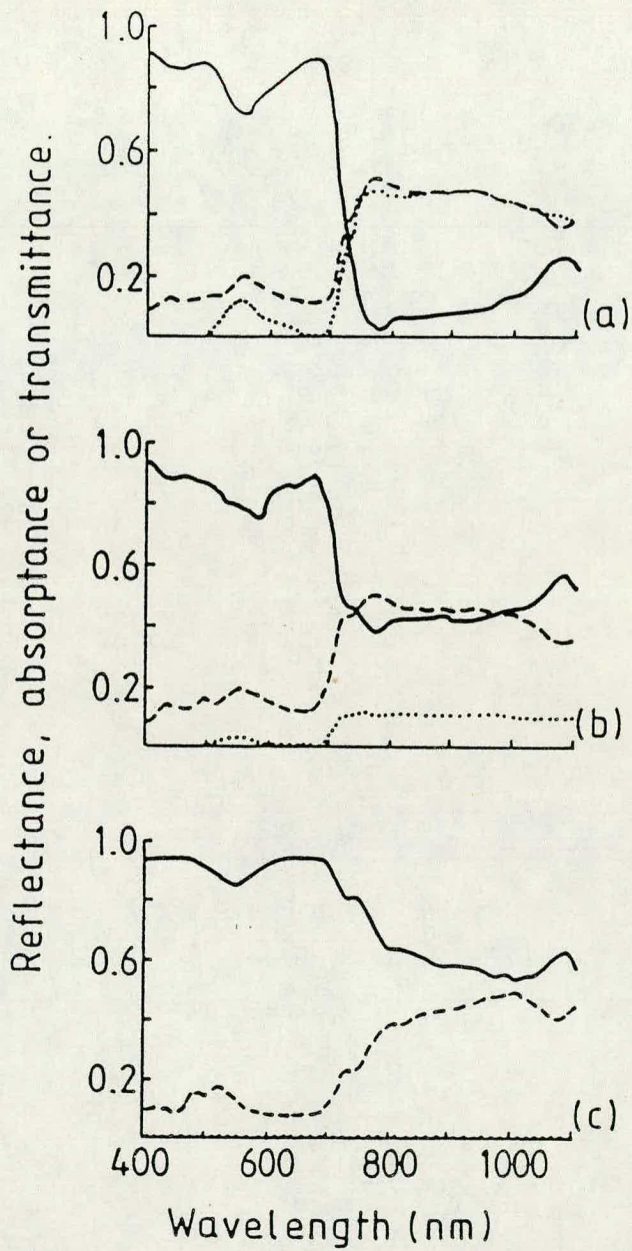


Fig. 4.3.2 The optical properties of *C. colocynthis* (3 leaves); the absorptance (solid line), reflectance (dashed line) and transmittance (dotted line). (a) the intact plant leaf, (b) vaselined and (c) the cardboard model.

4.4 Discussion

It was shown in section 4.2.4 that the leaf posture had practically no effect on g_a for an isolated leaf, but when the leaf replica was mounted within the canopy g_a increased with increasing leaf angle from the near-horizontal to the vertical position. The independence of the heat loss, in forced convection, on the leaf posture has been reported by several workers (e.g. Thom, 1968; Vogel, 1970). Angle has been found to affect substantially the heat transfer from leaves only when they are long and narrow (Parkhurst *et al.*, 1968).

The presence of lobes on leaves, as on *C. colocynthis*, was reported to have two features as far as the heat transfer is concerned; they increase the heat dissipation and reduce the dependence of that on the leaf angle (Vogel, 1970). Vogel ascribed the increase of the heat loss to the breaking up of the boundary layer around the leaf caused by the leaves' lobes.

The presence of other leaves may have two effects. Firstly, some degree of shelter is likely to occur and this would reduce the transfer of heat from a leaf in a sheltered position, the sheltering effect was reported by several workers (see Parkhurst *et al.*, 1968; Thom, 1971). Secondly, the roughness of the neighbouring leaves is likely to promote turbulence and lead to mixing between the air above the plant and in the spaces between the leaves. This might increase heat transfer in some cases, depending on the location and posture of the leaf, as happened in the present experiments when g_a was increasing with increasing leaf angle in the case of the leaf held within the canopy.

In the field, it is sometimes observed that almost all the leaves adopt a vertical posture or so (see the frontispiece). The increase in roughness that this constitutes may well increase aerodynamic conductance, though the effect on the shortwave radiation absorbed may be a more important influence on the energy balance (see Chapter 5).

The difference in size between the models does not appear to have been sufficiently large to cause much overall difference in the exchange rates and if anything it is the smaller leaf, not the larger one as expected, that has the lower conductance. This can be ascribed to the magnitude of lobing on the leaf as the older the leaf becomes, the more it becomes lobed. When the characteristic dimension, d , was measured there turned out to be little difference between the two leaves.

Although the calculated g_a'' and observed g_a agree quite well at low wind speed when the leaf was vertical, in the near- horizontal case the observed g_a was less than the calculated, especially in the mature leaf. This might be due to the sheltering effect at the low wind speeds where the boundary layer turbulence is not enough to promote heat loss, especially when the leaf is so close to the ground. At higher wind speed (between 2 and 3 ms^{-1}) the heat transfer rate was fast enough to put the expected and the observed g_a in good agreement. The departure between the two at the much higher wind speed might be due to the transition from a laminar to a turbulent boundary layer at high wind speed which increased the rate of heat loss so as to exceed the calculated values.

It should be mentioned that the plant leaf replica is only an approximate representation of the real plant leaf, particularly in the case of *C. colocynthis* leaves in which the surface roughness is difficult to represent on the brass. A consequence of this is that the boundary layer conductance of the model may not be the same, in absolute terms, as that of the real leaf. Sheltered zones on the leaf may experience, locally, lower-than-average conductances while exposed zones may display higher conductances. In general, there might be an overall greater roughness and consequently more turbulence and a higher conductance.

It has been mentioned that desert plants often display low absorptance to the incident shortwave radiation and when *C. colocynthis* is compared to absorptance of plant leaves of representative green leaves reported by Ross (1975) they showed low absorption in both shortwave and in the near infra-red. The shapes of the reflectance, transmittance and absorptance are similar to those reported by Gates (1980).

The optical properties of *C. colocynthis* unvaselined and vaselined leaves were similar in the shortwave part of the solar spectrum. Similar results were reported by Thorpe and Butler (1977) who found no significant differences between the absorption to the solar radiation between unvaselined the vaselined apple leaves. In the near infra-red part of the solar spectrum the difference between the unvaselined and the vaselined *Citrullus* leaves is more pronounced. Although the reflectance curves for the two treatments are of similar shape, the transmittance ones are not. The vaseline coat

resulted in higher absorptance of the incident near infra-red radiation. Thorpe and Butler (1977) found that the vaselined leaf had a higher transmittance than the untreated leaf when they measured the spectral properties of the vaselined and non-vaselined leaves.

Once the absorption values appropriate for the leaves and models in growth rooms or outside have been established, they may be applied to the calculation of the leaf energy balance outlined in Chapter 2.

CHAPTER 5

LEAF MOVEMENTS

Leaf movements in desert species are widespread particularly among those plants with relatively large leaves. Numerous authors pointed out the significance of leaf posture in reducing the load of incident energy on the leaves (e.g. Wainwright, 1977; Gates, 1980). Others have found movement to be associated with water stress (Dubetz, 1969; Forseth & Ehleringer, 1980).

C. colocynthis leaves growing indoors exhibited such movement as mentioned before. A nearly vertical posture of the leaves was noticed in plants growing in the natural habitat.

As was shown (Chapter 4), vertical orientation promotes the heat loss from the plant leaves and presumably reduces the interception of solar isolation.

As far as I know, such leaf movements have not been reported before in the literature for *C. colocynthis*. Therefore, in this chapter I describe an attempt to characterise in a preliminary way those leaf movements to assess the effect on them of ambient temperature and soil moisture.

5.1 Method

Ten potted plants were grown at 30 °C in the Fisons growth cabinet (for description, see Chapter 3). The experiment was carried out when the plants were 4 weeks old

and their main axis was still vertical. Five plants were assigned to each treatment at random, and set out in a row, distributing treatments at random. Plants received an average incident radiation of 500 W m^{-2} . The five plants assigned to the treatment 'water-stressed' were not watered during the three days prior to the experiment while the others were kept watered to 'field capacity' throughout the experiment. During the experiment, the water-stressed plants were watered with 100-150 ml of tap water on the appearance of any sign of wilting. One leaf of the first two leaves which were fully expanded was chosen on which to observe any movements. Two angles were measured: the petiole-to-stem angle (A), and the leaf-to-petiole angle (B) as shown in Fig. 5.1. The angle width was measured by fitting wire to the angle and determining the wire angle by using a protractor. Also, the plants were photographed daily against a grid.

The leaf temperature of each group of the plants was sensed; 3 leaves of each treatment were sampled by using 42 SWG copper-constantan thermocouples. The wet bulb depression was taken daily, using the Assman psychrometer.

The experiment was run at a range of ambient temperatures, $30-45^{\circ}\text{C}$, increasing in steps of 3°C each day.

To investigate whether the plant leaf possesses an specialised structure to control the leaf movements, as reported for other species, fresh sections at the base of the leaf petiole and at the joint of the stem-petiole were made using a freezing microtome, and examined using the light microscope.

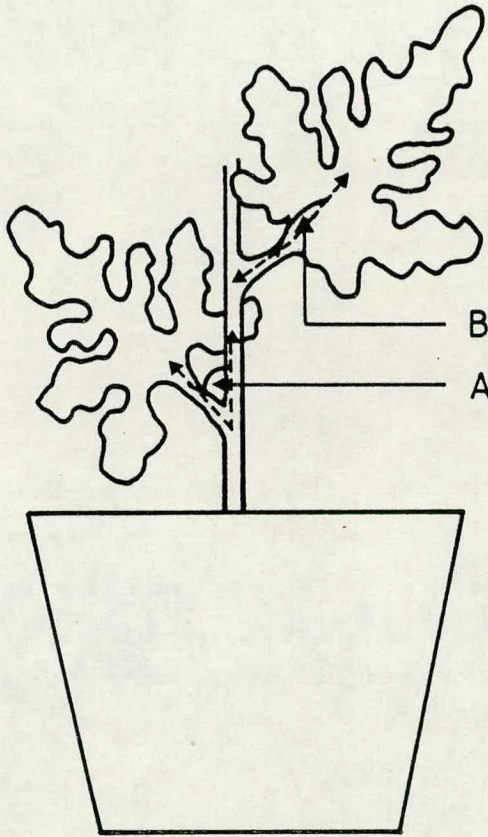


Fig. 5.1

A diagram of the angles measures; A, the petiole-to-stem angle; and B, the leaf-to-petiole angle.

5.2 Results

In the water-stressed plants, the petiole-to-stem angle significantly decreased at an ambient temperature of 39°C at $p=0.05$ (Fig. 5.2). As the stem at this stage is vertical, this angle brings the leaf progressively towards the vertical. The other angle did not display any significant changes at $p=0.05$ (Appendix C.1 for the analysis of variance). Neither angles (A and B) in the well-watered plants displayed any statistically significant change (Appendix C.2). From plate 5.1, it can be seen that leaf movements ranged from a horizontal to a nearly vertical posture, increasing with the ambient temperature. No attempt was made to vary temperature or VPD separately, and the leaf-air VPD increased over the six days along with temperature, as it might also do in the field (Fig. 5.2a and b). Leaf temperatures for the water-stressed and the well-watered plants were always below that of the ambient temperature but the water-stressed ones were $2-4^{\circ}\text{C}$ higher than the well-watered plants. Interestingly, in both treatments, a measurable cooling of the leaf occurred at relatively low ambient temperatures.

Plate 5.2 shows transverse and longitudinal sections of petiole and stem, including views of their junction. The petiole is hollow (Plate 5.2.D & F). At the point of the junction with the stem there is an external protuberance on the abaxial side of the petiole, which will be referred to as pulvinus, (Plate 5.2.A). The tissue in this region is made of large, thin-walled parenchyma cells (Plate 5.2.B).

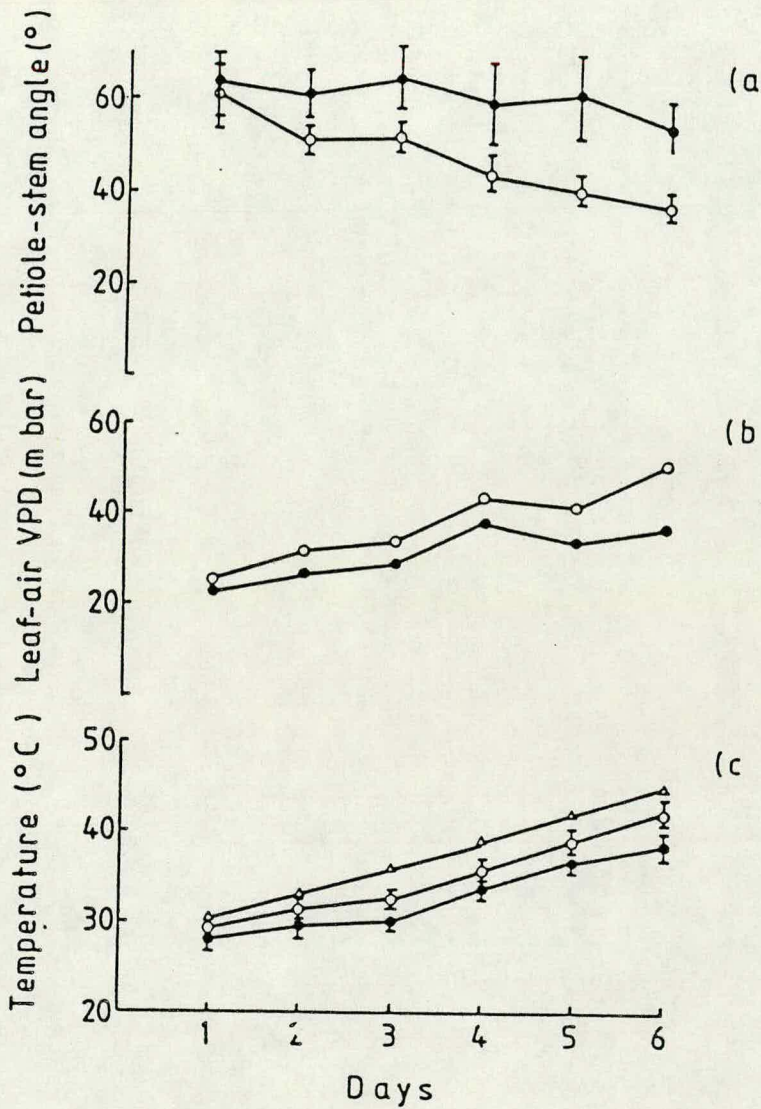


Fig. 5.2

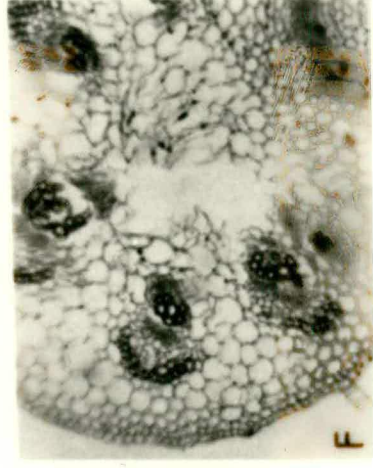
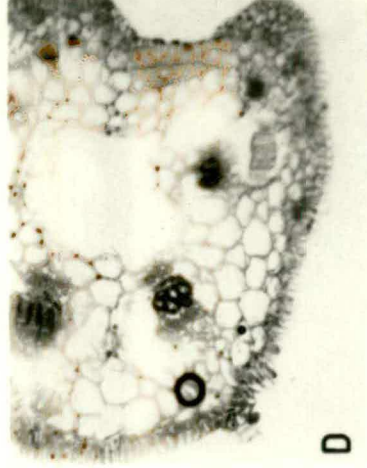
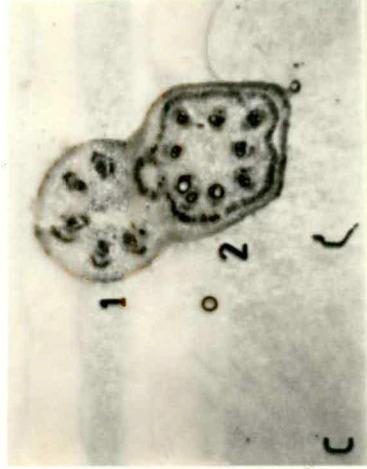
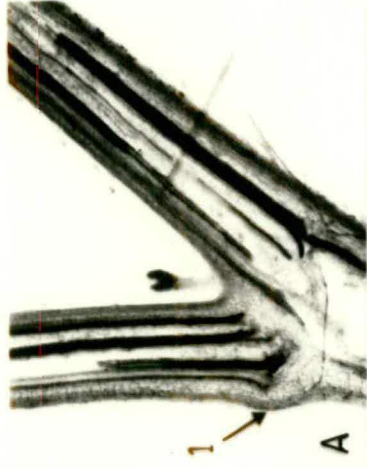
Shows the petiole-to-stem angles (a); leaf-air VPD (b); and the leaf temperatures (c); for the dry treatment (the open circle) and the wet treatment (solid circle). The open triangle denotes the ambient temperature in each day. Bars show the standard errors of leaf temperature taken hourly and averaged over the course of the whole day. the incident radiation was 500 W m^{-2} .



Plate 5.1

Leaf movements of the plant. It can be seen that most leaves in the water stressed treatment adopted a nearly-vertical position at higher ambient temperatures. The treatments are labelled on the pots as W = well-watered, D = water-stressed. The temperatures are 30, 33, 36, 39, 42 and 45 °C in rows beginning at the bottom row.

Plate 5.2 Anatomy of the pulvinus, petiole and stem. A, petiole-to-stem junction. L.S., to show pulvinus (1) and vascular strands; B, high power of pulvinus tissue; C, TS at the petiole-to-stem junction; the petiole (1) is hollow, the stem is angular; D, the petiole half-way along its length; E, stem TS at internode; F, TS of petiole near its base.



5.3 Discussion

Several authors have reported leaf movements in plants during water stress (e.g. Dubetz, 1969; Shackel & Hall, 1979). Ehleringer and Forseth (1980) pointed out that leaf movements are of adaptive value for plants with limited moisture. As a result of the leaf movements the absorbed energy may decrease and water loss may be reduced. The ability of *Lupinus arizonicus* to survive in the Sonoran Desert was ascribed to the direct response of the leaf movements to changes in the plant water status (Forseth & Ehleringer, 1980). In the present work, the variation in angles over the six days and between treatments cannot simply be related to temperature or leaf-air VPD. It is more likely to be determined by the water status of the tissue, since it was so much more apparent in the plants from which water was withheld.

Most leaves which display movement at the petiole-to-stem angle possess specialised tissue, at this point, to form the pulvinus (Esau, 1977). The change in the size of the upper and the lower cells of the pulvinus control the leaf movements. Some authors prefer to use the words extensor and flexor regions of the pulvinus for the upper and lower cells of it respectively (e.g. Schrempf, Satter & Galston, 1976; Setter, 1979). In the lifting phase the extensor cells expand by turgor and contract during the closure, while the flexor cells respond in the reverse manner. It is likely that leaf movement in *Citrullus* is controlled by such turgor regulation. The large thin-walled cells of the pulvinus would have to expand to make the petiole vertical. Since one would expect a

general loss of turgor with tissue water stress it is necessary to postulate that either there is 'active' turgor regulation involving a pumping mechanism analogous to that of the stomatal guard cells, or that the elastic properties of the cell walls on adaxial and abaxial surfaces differ so that there is a different turgor pressure between the surfaces when tissue water potential falls. Satter (1979) reviewed findings about the relation between the leaf movements and the flux of certain elements to the cells involved in the movement. Fluxes of K^+ and Cl^- are often involved. Schrempf et al. (1976) reported that the change in the size of the pulvinal cells in *Albizia julibrissin* involving Cl^- and K^+ fluxes. Inhibition of leaf movements of *Lupinus arizonicus* was induced by increasing concentrations of Lanthanum, a known ion transport inhibitor (Wainwright, 1977).

In the desert, adopting a leaf posture parallel, or nearly so, to the solar radiation flux, particularly during midday, has a significant effect in reducing the energy load on the leaves. The effect of angle on the interception of energy by a plane surface from a cloudless sky has been calculated, and results are given by Robinson (1966).

Although in the present experiment *Citrullus* leaves did not display movement to a completely vertical position, on other occasions in the laboratory and the field they were observed to do so (see the front page). Modification of the leaf energy balance for a leaf standing at an angle of 70° instead of in a horizontal posture was reported to cause a remarkable reduction in the leaf temperature and the transpiration rate

of the desert shrub *Atriplex hymenelytra* (Mooney et al., 1977). Gates (1980) reported that the temperature of *Erythrina indica* (Sydney, Australia) leaves which were adopting a nearly vertical position was 4-6 °C above that of air while other leaves on the same plant but with a horizontal posture were 10-12 °C above that of the ambient.

In conclusion, the movement of the leaf in *Citrullus* is determined by events within the tissues at the petiole base. The large parenchyma cells resemble those reported for other pulvini (notably in Legumes). To make the pulvinus operate, there must be changes in turgor between adaxial and abaxial tissues, and for this to be ecologically 'useful', these changes must be activated by stress. It is likely that water stress activates the process (rather than temperature stress), as the response is much more apparent in plants from which water is withheld.

CHAPTER 6

ROOTS DEVELOPMENT AND PLANT
LEAF GROWTH IN A
CONTROLLED ENVIRONMENT

It has been shown by researchers that 'under-temperature' plants transpire at a high rate and cool down their organs to a temperature below that of the air (Lange, 1959; Gates, 1968; 1980). Therefore summer active desert plants which adopt this mechanism to survive the hot dry summer must have certain adaptive features to obtain enough water to sustain the transpiration rate and thus prevent the plant overheating.

Although survival of such plants is dependent mainly on their adaptation to the harsh environment during the vegetative phase it is also crucial that they are able to establish themselves at the right place and the right time. Some authors ascribe the success of these plants to the above ground adaption, *per se*, but it is important not to overlook the less obvious adaptations that occur underground (Evenari *et al.*, 1976; Kummerow, 1981).

In this chapter an experiment on the development of the root system of *C. colocynthis* held at different water levels will be reported. The aim is to assess the role of the root system in exploiting the water resource and thus sustaining the transpiration at a high rate. In particular the experiment was designed to see how the pattern of root growth is determined

by the water table. At the same time growth rate of leaf area was assessed.

6.1 Background

It is well known that perennial desert plants develop deep and extensive roots enabling them to absorb water from a large volume of soil and far away from any root competition for water. Deep rootedness in perennial desert plants has been reported by several workers (Maximov, 1929; Migahid, 1954; 1961; Evenari *et al.*, 1971). Evenari *et al.* (1971) found that roots of some desert shrubs and dwarf shrubs are adapted to the moisture conditions of the soil, in such a way that a shallow root system is developed when the surface water is adequate. These roots do not penetrate more than 0.5 m and restrict their development to the wet upper layer producing an extensive lateral root system. Similar rooting characteristics in perennial shrubs were reported by Solbrig *et al.* (1977). The root distribution of desert plants is determined by the availability of the water. Solbrig *et al.* (1977) identified three sources of soil moisture 1) the water in the upper 20 cm of the soil - roots with fast uptake can remove water from this layer as it quickly dries out, 2) water at intermediate depth which can be absorbed over a longer period due to reduction of the evaporative loss and 3) water in the depressions and wadis which is abundant and relatively permanent but can be reached only by an extensive system of tap roots.

Maximov (1929) reported that roots of some desert plants may penetrate to a depth of 10 m and more till they reach the water table where they start to branch and explore larger volumes of soil. Other desert species may develop two kinds of root system: the main tap roots which penetrate deeply and the upper lateral roots which are superficial, spreading over a large area (Evenari *et al.*, 1971). Walter (1979) reported that a long tap root developed only for plants which depend on the ground water. The extensive root system is one of the adaptive characters of the perennial desert plant while the annuals have a different strategy to assure the optimum water absorption (Evenari *et al.*, 1971; Mulroy & Rundel, 1977). Surprisingly, some desert plants can form special fine roots only a few hours after rainfall or showers (Oppenheimer, 1960; Evenari, 1971). Evenari *et al.*, (1971) found that old roots which are lignified and covered by cork layers develop rootlets whenever the soil is wet. Moreover, the root hairs of these desert plants cover the young roots from the base to the tip as they are the most active in absorbing elements and they are not restricted to the growing and differentiating zone at the tip.

Storage of water in the plant root or shoot system is well known in perennial desert plants particularly among the succulent species. Zohary (1961) reported that the thick tap root of *C. colocynthis* may reach a diameter of 5-7 cm and could contain a large amount of water enabling the plant to survive dry conditions.

It was noticed quite early that desert plants develop a

high proportion of root to shoot under the dry conditions (Maximov, 1929; Oppenheimer, 1960; Migahid, 1961). This high root to shoot ratio might favour 'under temperature' or 'water spender' plants (Levitt, 1980 defined them as those plants which can avoid drought by absorbing water sufficiently rapidly to keep up with the high water loss). Clearly, it would be advantageous to increase water uptake thus having an efficient root system and the facility for rapid growth into deeper soil. Larcher (1980) reported that seedlings of woody plants in dry regions have tap roots 10 times as long as the shoot. The root to shoot ratio is observed to increase with increasing degrees of drought in dry regions (Fischer & Turner, 1978; Larcher, 1980) while in the wet regions, plants have more shoot than root (Walter, 1979). Kummerow (1980) pointed out that this ratio showed remarkable seasonal change and due to this seasonal fluctuation, the extent of the above-ground biomass should be interpreted with caution. The high root-shoot ratio can, however, be viewed either as part of the 'water-spender strategy' to maintain a high transpiration or part of water saving 'strategy' when coupled with other above-ground adaptations (Etherington, 1982).

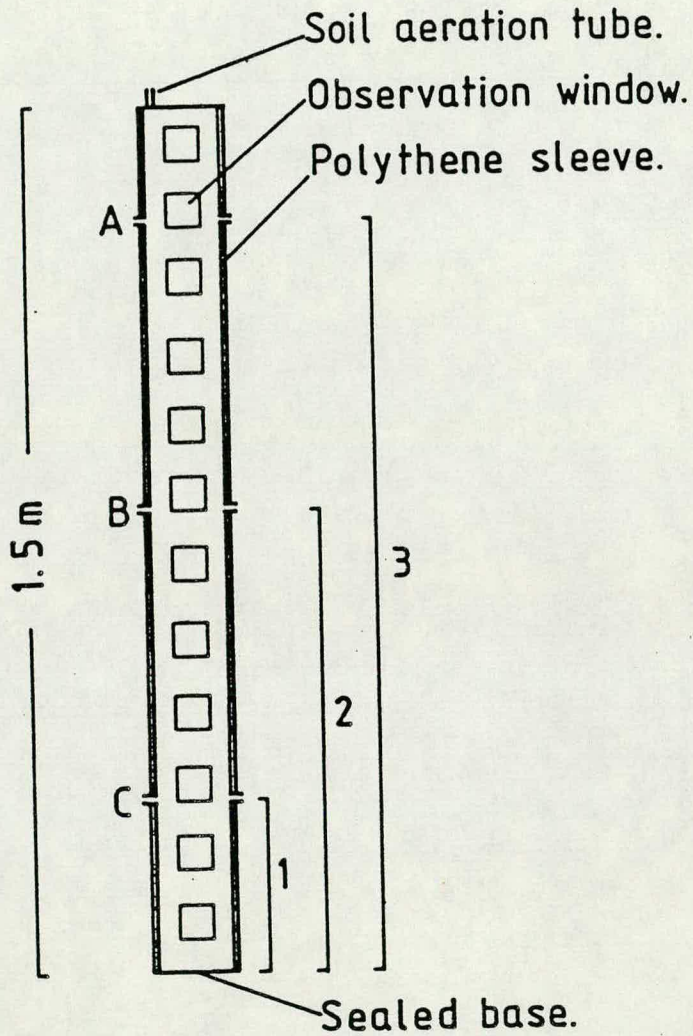
6.2 Methods

Various methods have been employed to study root growth and distribution. A review of these methods is available in Böhm (1979). In the present study it was convenient to use PVC tubes (1.5 m length and 7.5 cm diameter). Twelve

observation windows (5 x 6 cm) were cut in each tube. A diagram of one of the 15 tubes which was used is shown in Fig. 6.1. Double thickness polythene sleeves were inserted in the tubes and perfectly sealed at the bottom. The roots were thus not in contact with the PVC, which sometimes releases toxic materials, but with polythene which is relatively inert. A perforated rubber tube (1.6 m length and 7 cm diameter) was inserted into each sleeve before filling with the soil mixture (70% sand + 30% garden soil and pH 7.2). The purpose of the rubber tube was to promote soil aeration. The 15 tubes were set up in the growth room (Department of Forestry and Natural Resources) with photon flux density of $450 \mu\text{mol m}^{-2}\text{s}^{-1}$ in the waveband 400-700 nm at ambient temperature 30-32 °C. They were held slightly inclining in such a way that the root system growing vertically downwards pressed against the observation windows and could thus be assessed. The observation windows were covered by black polythene sheet except when observations were being made. A wooden board with 15 holes in two rows (8 and 7 holes) was used to hold the tubes at their upper rim and to form a support on which the shoot system could develop and trail in a natural manner.

Fifteen *Citrullus* seedlings 3 weeks old were transplanted into the tubes and were kept well watered over the first week until the seedlings were well-established.

Three different water levels were applied; the dry, intermediate and wet treatment as shown in Fig. 6.1. Treatments were randomly distributed within the room. Holes A, B and C were drilled to determine the water level and to



Water table depth from the top as follows:

1 = 120 cm (dry treatment)

2 = 70 cm (intermediate treatment)

3 = 20 cm (wet treatment)

A, B and C represent the drainage hole for each treatment.

Fig. 6.1 Shows the PVC tube which was used for the root growth experiment.

facilitate watering the tubes to the point of overflow from these holes. Leaf area was estimated by using a relation between leaf length and logarithm of measured area. For observing the development of the root system the modified line intersect method as suggested by Tennant (1975) was used, using a grid (5 x 6 cm and 0.5 cm² grid unit). The grid was fitted on the observation window and the number of root intersections with the vertical and horizontal line were counted so that the total root length in that window could be assessed by applying the equation

$$LR = n \times c \quad (6.1)$$

where LR = the root length

n = the number of intercepts

c = length conversion factor (c = 0.3928 for a grid with 0.5 cm² unit)

In the day prior to harvesting the leaf water potential (ψ) was measured on leaf discs using the triple psychrometer chamber (Dixon, 1982). The pressure bomb could not easily be used because of a viscous secretion that appeared at the cut surface of a petiole.

For washing the root system the polythene sleeve was pulled from the PVC tube and laid in a small plastic pond. Length of tap root was measured directly while the secondary and fibrous rootlet length was estimated by using the method proposed by Newman (1966). Fig. 6.2 contains a sketch of the three types of root system; tap roots, secondary and fibrous.

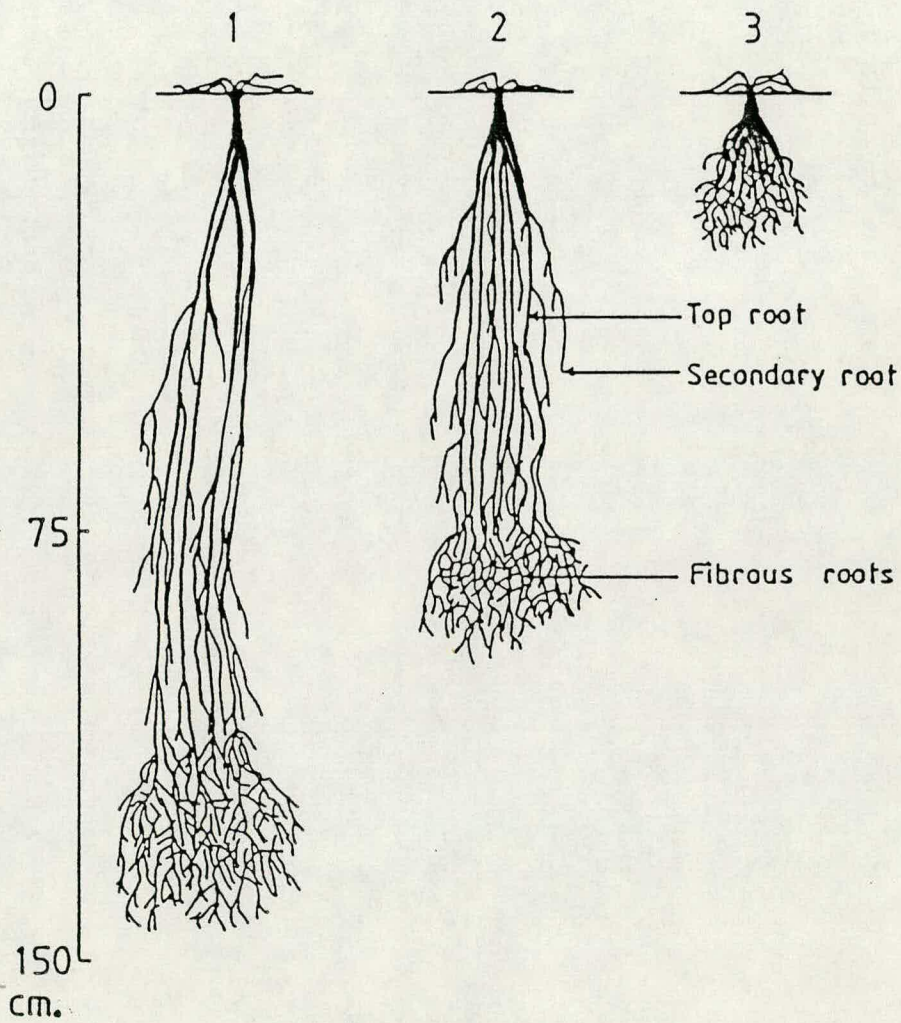


Fig. 6.2 A sketch resembling the root system in the dry (1), intermediate (2) and the wet (3) treatments.

Although the tap roots were not as thick as the mature tap roots seen in the wild, all roots growing from the radicle of the plant eventually develop to form a tap root. Thus they are referred to as tap roots. The rootlet (secondary and fibrous) length was determined by putting roots in a rectangular dish of suitable size (6.5 x 13.5 cm). A plastic sheet marked with random straight lines was put under that dish. The number of intersections between the root and the lines was counted. Thus the total root length can be found as follows:

$$LR = \frac{\pi n A}{2H} \quad (6.2)$$

where LR = the total root length

n = the number of intersections between the root and the straight line

A = the area of the rectangle

H = the total length of straight lines.

To determine the soil moisture content SMC in the tubes after ending the experiment one tube of each treatment was divided to 15 sections. In each section, the fresh weight was immediately determined and then they were dried in the oven at 90 °C to find the dry weight. So the soil moisture content was calculated as follows;

$$SMC = \frac{\text{Fresh weight} - \text{dry weight}}{\text{dry weight}} \times 100 \quad (6.3)$$

The leaf area at the end of the experiment was

determined by using the leaf area meter (Li-3000, LiCor, Nebraska).

The shoot and root dry weight was found by putting the plant material in the oven at 80 °C for at least 24 hours and weighing using a precision balance.

The mean area relative growth rate over the time interval (ARGR) was calculated by applying the equation that was used by Evans (1972) and Russell and Grace (1979) as follows:

$$ARGR = \frac{\ln A_2 - \ln A_1}{t_2 - t_1} \quad (6.4)$$

where A_2 and A_1 are leaf areas at time t_2 and t_1 respectively.

Although some workers have used leaf area to leaf fresh weight to find leaf specific area SLA (see e.g. Larcher, 1980) this is not appropriate as the leaf fresh weight is changeable according to the environmental conditions. Therefore, to calculate SLA the more usual equation given by Hunt (1982) was used:

$$SLA = \frac{L_A}{L_W} \quad (6.5)$$

where L_A is the leaf area and L_W is the leaf dry weight.

Also at harvesting an image of the main axis of each plant was made on 'ozalid' blue-print paper. The soil pH was determined for a sample of each treatment by the end of the experiment.

6.3 The results

Root development during the experiment is shown in Fig. 6.3. It can be seen that in the treatment having the lowest water level (the dry treatment) the roots were growing more rapidly than the intermediate and the wet treatment respectively. By the third week after the application of the three water levels, roots of the dry treatment reached the level 1.2 m down, while the development of roots for the others was more or less restricted to the zone above the water level and did not proceed to deeper zones particularly in the wet treatment. Once the tap root reached the soil moisture it became branched forming numerous fibrous roots (plate 6.1). Although the tube system facilitated the observations on rooting depth, it was found at harvesting to have been less useful, indeed misleading, on the question of root quantity. This is because the tap roots are readily visible at the windows because the tube slopes, but the development of the other, fibrous, roots in the rest of the soil cannot be followed.

Root length at the end of the experiment is shown in Table 6.1. The driest treatment where the water level was very low (130 cm) had the longest tap root. However, there was no significant difference between means of the dry and the intermediate treatment. But plants in the intermediate treatment developed significantly more fibrous roots. Interestingly, in the wet soil treatment the tap root became more branched and the tap root number was significantly higher than in the dry treatment.

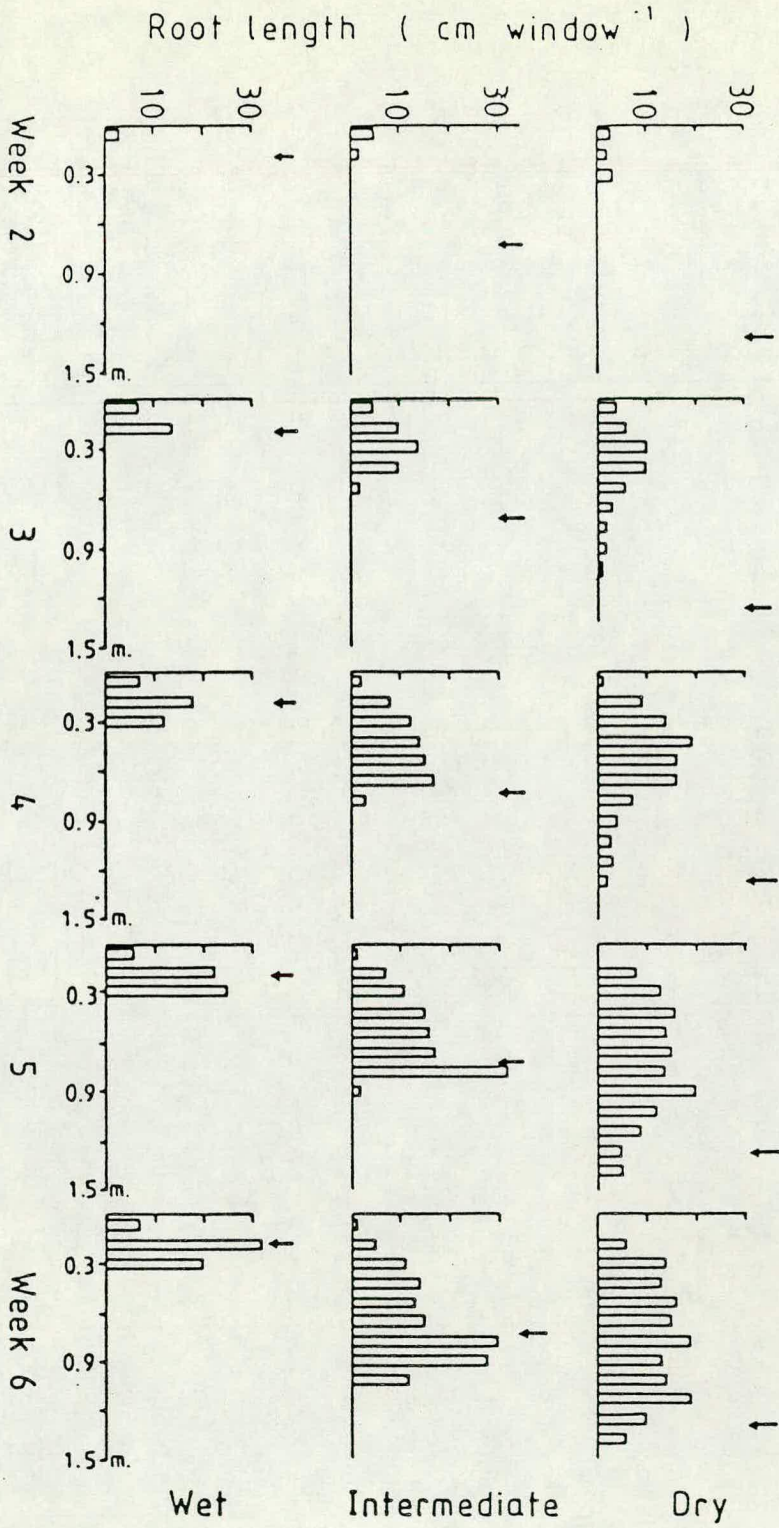


Fig. 6.3 Root development after applying the 3 water levels at the end of week 1. The bars represent root length in each observation window. The arrows show the water level in each treatment.



Plate 6.1 The branching of the root system in the moist zone of the soil in window number 7 (see Fig. 6.1) counting from the top. The intermediate treatment is on the right, and on the left is the corresponding window in the dry treatment where the branching is much less.

Variate	Treatment		
	Dry	Intermediate	Wet
Tap roots, length (total)	273 ab	338 b	145 a **
Tap roots, length (mean)	74.3 a	51.9 b	16.2 c **
Secondary roots, length	166 a	203 a	149 a
Fibrous roots, length	1084 a	2530 b	1220 a *
Root system, total length	1693 a	3280 b	1317 a *
Tap roots, number	3.6 a	6.7 ab	9 b *

** : the significant difference at $P = 0.01$

* : the significant difference at $P = 0.05$

Means share the same letter if there is no significant difference between them.

Calculations of analysis of variance were done by using the Genstat statistical package. The difference between the treatments were found according to Duncan's multiple range test.

TABLE 6.1: Root length (cm). Means of each part of the system is shown for each treatment. The tap roots' mean length was found by dividing the tap root total length by its number of branches.

Table 6.2 shows the root system dry weight. Tap roots in the wet treatment had the highest dry weight. However there was no significant difference between the wet and the intermediate treatments. For the total weight of roots both treatments were significantly higher than the dry treatment. But in the dry treatment roots had more length per weight in the tap and secondary roots than the other treatment (Table 6.3). Although the dry weight of the shoot system in the intermediate treatment was higher than that of the other two treatments for all shoot variates, the dry treatment unexpectedly had the higher specific leaf area SLA (Table 6.4).

The estimated area relative growth rate during the course of the experiment is shown in Fig. 6.5. From that it can be seen that leaf development was affected by the different water levels. In the second week the leaf area growth was about equal for all treatments but it was the wet treatment which displayed the lowest growth rate in the second half of the experiment, with the intermediate treatment showing the highest rates. The type of leaves produced was also influenced by the treatment. In wet conditions the leaves were more dissected and somewhat elongated (Fig. 6.6). A consequence of this is that use of the generalised regression of leaf length against leaf area will thus lead to systematic error when comparisons are being made between treatments. The extent of the errors can be roughly assessed by inspection of Fig. 6.7 in which data from some leaves of this experiment are displayed in relation to the generalised regression. Unfortunately, new, treatment-

specific regressions could not be developed retrospectively as the quantity and spread of data are not sufficient. Despite this difficulty it can be said that in the wet treatment the ARGR fell to zero at the end of the experiment and the plants developed flowers. In the other treatments the ARGR fell somewhat but no flowers were produced in the dry treatment and only one plant flowered in the intermediate treatment (Table 6.4).

The water level had an effect on the leaf water potential, the lower it was the lower was ψ . However, the water stress was by no means extreme (Fig. 6.8). The soil pH in each was 6.16, 6.12 and 6.2 for the dry, intermediate and the wet treatment respectively.

Variate	Treatment		
	Dry	Intermediate	Wet
Tap roots (total)	0.369 a	0.769 b	0.779 b *
Fibrous	0.494 a	1.081 b	0.654 a *
Secondary roots	0.0286 a	0.0402 a	0.0385 a
Total	0.891 a	1.889 b	1.471 b **

TABLE 6.2: Dry weight of roots system (g)

Variate	Treatment		
	Dry	Intermediate	Wet
Tap roots	740	439	186
Fibrous	2194	2340	1865
Secondary	5804	5049	3870

TABLE 6.3: The root lengths/mass (cm g^{-1})

Variate	Treatments		
	Dry	Intermediate	Wet
Leaves (g)	1.59 a	2.59 b	2.17 b *
Petioles (g)	0.202 a	0.356 a	0.234 b
Tendrils (g)	0.0254 a	0.0452 a	0.0282 a
Stems (g)	0.495 a	0.836 b	0.830 b *
Shoot system (g)	2.32 a	3.83 b	3.26 ab *
Plants flowering (number)	0	1	3
ARGR (mean) (wk^{-1})	0.555 ab	0.628 b	0.518 a *
Final leaf area (cm^2)	341 ab	521 b	285 a **
Number of leaves on main axis	17.4 a	17.2 a	14.2 a
Number of shoot tips	6.6 a	8.8 a	6.7 a
SLA ($\text{cm}^2 \text{ g}^{-1}$)	217.1 a	203.1 a	129 b **
Root to shoot ratio	0.384	0.493	0.451

TABLE 6.4: Mean attributes of *Citrullus* plants grown in three treatments.

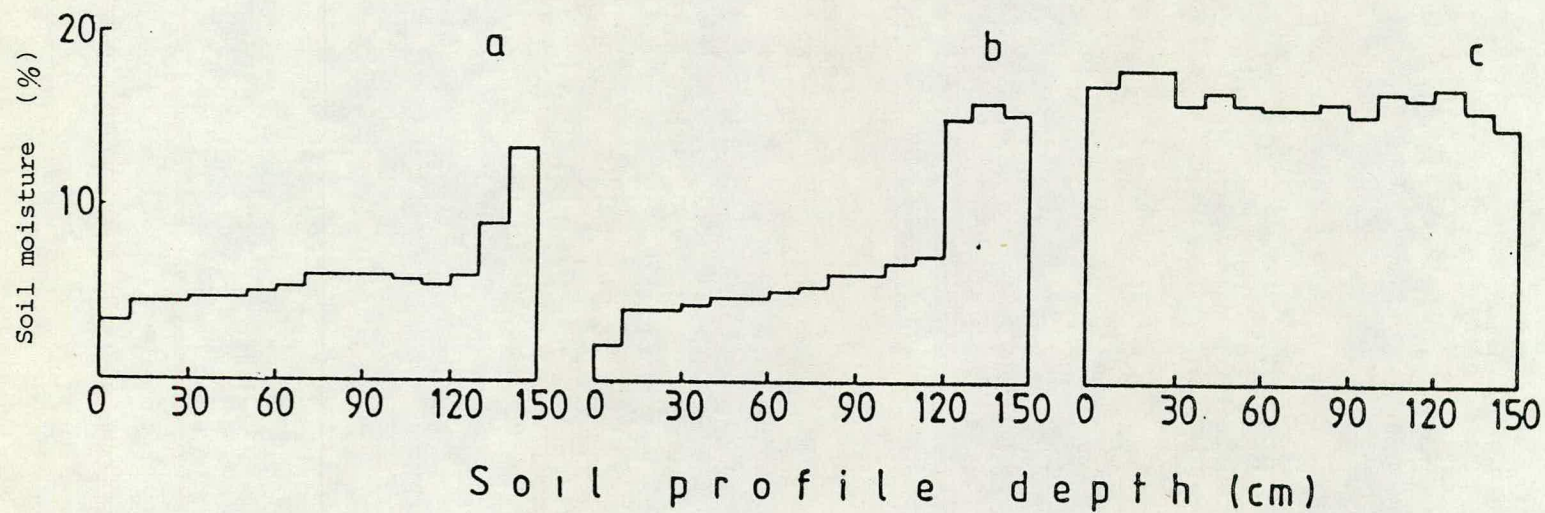


Fig. 6.4 The soil moisture content in one tube of each treatment, (a) the dry, (b) the semi-dry and (c) the wet treatment.

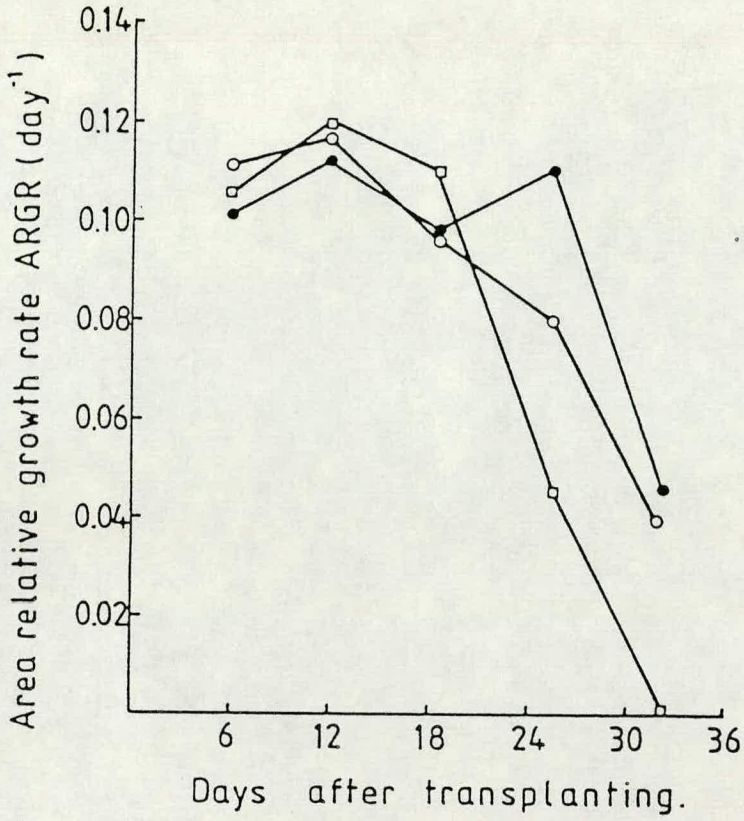


Fig. 6.5

The estimated ARGR for the first 5 weeks of the experiment. The treatment was started at day 12. Data of the measured leaf area at the end of the experiment is not included. Open circles denote the dry, solid circles the intermediate and open squares represent the wet treatment.

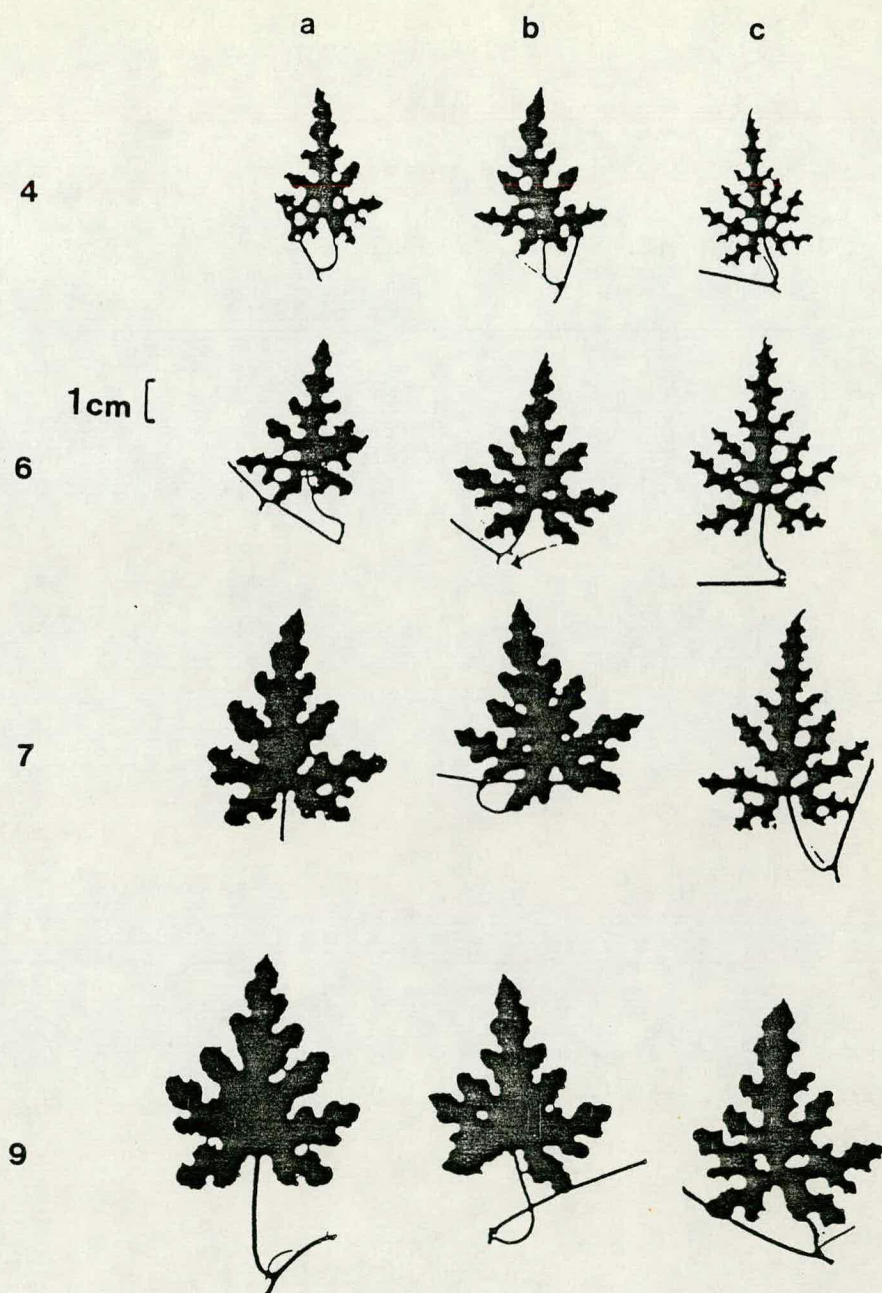


Fig. 6.6

Representative examples of the leaves of plants grown at (a) dry; (b) intermediate, (c) wet treatments. The numbers in the column represent the leaf stage counting from the youngest leaf on the main axis.

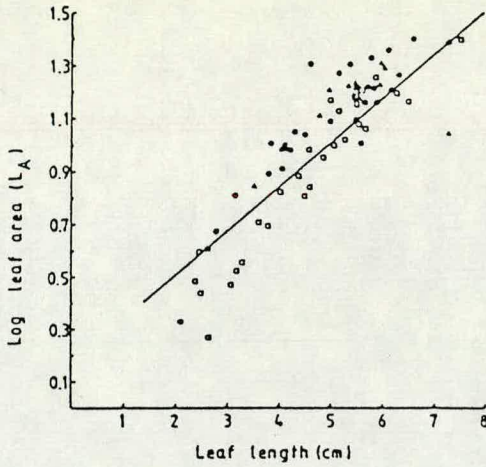


Fig. 6.7

To find the estimated leaf area from the lengths, 60 leaves were measured for their length and area using plants grown before the experiment. A regression equation of the leaf and log L_A was calculated. The relationship is described by the equation

$$Y = 0.1637 + 0.01686X$$

The points are samples taken from plants at the end of the experiment. The open circles denote the dry treatment ; triangle for the intermediate and open squares represent the wet treatment.

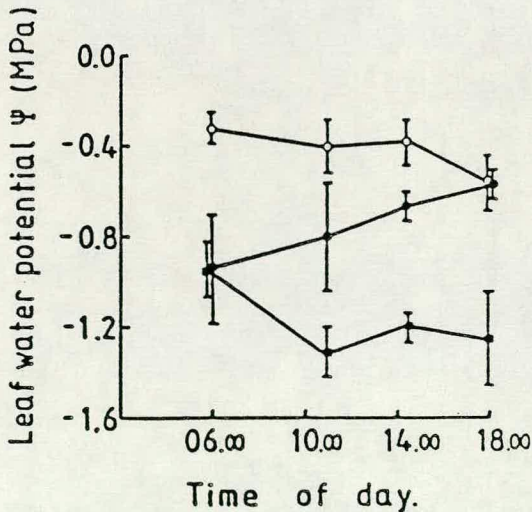


Fig. 6.8

Leaf water potential of the three treatments as measured on the eve of harvesting day. The wet, intermediate and dry treatments are represented by the open circles, solid circles and solid squares respectively. Each point is a mean of 3 leaf discs. The SE is represented by the bars.

6.4 Discussion

It has been demonstrated that the plant has the ability to develop a fast growing root system which appears to seek water. Tap roots grew vertically as soon as each root reached sufficient soil moisture it started to produce a massive number of fibrous roots to facilitate water uptake. This mode of development might be an adaptive strategy of such plants that inhabit depression and wadis where the soil moisture during the dry seasons falls but where there is always a subterranean supply. By having the ability to develop a tap root system able to reach the soil moisture, the plant has access to water even when atmosphere conditions are dry, and the upper soil levels are also dry. Such root development in desert plants is widespread as reported by several authors (e.g. Evenari *et al.*, 1971; Daubenmire, 1974).

As an adaption to dry conditions, plants growing in arid regions usually have a low SLA (Larcher, 1980; Fitter & Hay, 1981). In this species the SLA was low overall but in the dry conditions it increased instead of decreasing. The low specific leaf area is generally presumed to provide a water economy, as a thicker leaf contains more photosynthetic machinery and generally has a higher light-saturated rate of photosynthesis (Björkman, 1981). Thus, if all other things are equal, a thicker leaf displays a higher water use efficiency measured as carbon gained per mass of water transpired. In *Citrullus*, however, the response of leaf development to the applied shortage of water appears to have been more complex. The leaves developed with a high water level were considerably more dissected and

somewhat more elongated than those which grew at low water level. Such leaves, for structural reasons may require additional mass per area in the form of extra layers of cells and lignified vascular tissue. It may be argued that for a 'water spender', it is not advantageous to develop a finely dissected leaf. Only when the leaf is entire and large will it display a maximal r_a , and thus only then will its 'water spending' lead to cooling below the ambient air temperature. Thus, in low water treatment, the leaves developed in a manner which can be interpreted as an adaptation for leaf cooling. A finely dissected leaf lacks this adaption, and 'water spending' in such a leaf should lead to only little cooling below ambient. These ideas will be explored quantitatively in a later chapter.

The low root to shoot ratio in the dry treatment is also anomalous and requires discussion. It is however clear from the observations at the windows of the culture vessels (Fig. 6.3) that the root system in the dry treatment did develop rapidly at the start of the experiment, and was successful in reaching the wetter zones of soil. Perhaps the root/shoot ratio would not have been anomalous in the early part of the experiment. At the end of the experiment the root/shoot ratio might have been influenced by the shortage of nutrients in the very limited soil volume available to the 'wet' treatment. It is known that root to shoot ratios are generally high in nutrient poor conditions (Moorby & Besford, 1983). It is also important to realise that important changes in phenology occurred in the wet treatment; leaf growth

stopped and flowering began. Thus, it is not reasonable to make comparisons between treatments, since although plants were of the same age, they were nevertheless at different stages in their life cycle. Whatever the cause of the anomaly, it is clear that tap root system worked effectively, giving rise to a hydraulic architecture which is able to obtain water from considerable depth. The mechanisms involved in the development of this root architecture are not known. Some workers ascribe the rapid growth of the root under water stress to the ability of growing tip to maintain the positive turgor required for cell extension (Sharp & Davies, 1979). This can be achieved by osmotic adjustment (Greacen & Oh, 1972). On the other hand, the vertical development of the tap root may simply be a geotropic response. This is suggested by the way the roots were visible at the windows on the inclined tube. When the tap roots reach the moist soil they did not proceed in response to the geotropism, presumably being intolerant of the low oxygen concentrations in the flooded soil. Although in this experiment the roots did not grow into the water, and thus it is probably correct to say that root growth is intolerant of low oxygen concentration (Crawford, 1982; Kramer, 1983), it is clear that in the field the tap root is flooded completely in the wet season in the wadi areas. Thus the tissue itself must be able to tolerate flooding even though growth does not occur.

In nature the tap roots develop considerably as water storage organs (Zohary, 1961). In the experiment this did not have time to occur, although the treatments do display

variation in the length per weight of tap root, and this may be an indication of the advanced development in the wetter treatments.

The leaf area growth rate determined during the course of the experiment is subject to error as already mentioned. The extent of the error can roughly be assessed as follows: when the area of mature leaves on the main axis are plotted on the generalised regression line, it is seen that the area of the 'dry' treatment was probably underestimated by 20-30%. Referring to Table 6.4, the measured mean ARGR over the course of the experiment in the intermediate and dry treatment are higher than the wet treatment and is not qualitatively at variance with the estimated ARGR obtained from leaf lengths.

In conclusion, the work reported in this chapter has demonstrated the general features of root development in this species, showing how the plant is adapted to obtain water from great depths. More quantitative studies of hydraulic conductivity and storage capacity of the root system are desirable, though in long-lived perennials it is time consuming to grow material to a point where the roots bear proper resemblance to those in the field, and the length of the growth tubes in long term experiment should be extended to several meters. The degree of water stress in the present experiment was never very high, as a consequence of the way in which the root system so readily reached the water level.

CHAPTER 7

DETERMINATION OF LETHAL TEMPERATURES

In chapter 3 it was shown that irrespective of the ambient temperature, the leaf temperature of *Citrullus* did not exceed a certain limit (42.5°C). A similar result was reported for the plant by Lange (1959). In this chapter an experiment to determine the lethal temperature is described, aiming to aid assessment of the significance of the cooling response at high air temperatures.

Although Lange (1959) has already reported determinations of lethal temperatures for *Citrullus*, it was regarded^{as} important to confirm his finding, and to extend it to consider the duration of exposure as well as the temperature *per se*.

7.1 Background and technical review

In ecological and physiological studies it is important to determine the limit of heat tolerance of desert plants to understand how well these plants are adapted to the high temperature environments. In general, the lethal temperature is not easy to determine with a high degree of certainty. Levitt (1980) defined the lethal temperature for a plant as the temperature at which 50% of the plant is killed. This temperature does differ from species to species, the highest recorded killing temperatures of vascular plants being about $60-65^{\circ}\text{C}$ (Biebl, 1962 cited in Levitt, 1980).

Several workers have tried to determine lethal

temperature using quantitative methods following Sachs (1864), cited in Levitt (1980) either exposing the plant or part of it to hot air or immersing it in water at the required temperature. After the treatment plants are grown in normal conditions to permit observations of any change in the plant tissue during subsequent days or weeks. Levitt (1980) reviewed other methods workers have used to determine heat killing or heat tolerance temperatures of plants.

Lange (1959), in his trip to Mauritania, exposed leaves using a Dewar flask containing water at a known temperature. A branch or shoot system consisting of a bunch of leaves connected to the mother plant was immersed in the flask and hot water was added to increase the temperature in steps. The exposure temperature was counted as the mean of the beginning and the final temperature for a duration of 30 minutes. After 3 days the effect of the treatment on the leaves was observed. In other experiments Lange used a different technique using a blackened glass cylinder to enclose the plant shoot. Then a strong beam of light was directed onto the cylinder to increase its internal temperature. By using the water container method, Lange determined the heat resistance and killing temperature of several species growing in Mauritania and the tropical rain-forest in the Ivory coast. Among actual desert plants, Lange found that some of the species were very sensitive and damage occurred at a relatively low temperature, unexpected in view of the high temperatures to which they were exposed in nature. Lange (1959) observed serious damage to *C. colocynthis* leaves at 49 °C

when the water immersion method was used and at 52 °C in the hot air (complete death of the plant leaves occurred at 52 and 55 °C in the water and the hot air method respectively).

In recent years workers have tended to use solute leakage from the plant tissue as an indication of injury induced on the plant tissue. Probably, this method was first used by Lieberman *et al.* (1958) to investigate the chilling injury on sweet potato root. In this method the solute leakage takes place as a result of cell membrane damage. Wright and Simon (1973) used the same method to study the chilling injury on whole cucumber leaves. Other workers used small pieces of leaf tissue as did Patterson, Murata and Graham (1976) in a chilling injury study of *Passiflora* species. Some workers have used the leakage method to study the high temperature stress on plants. Onwueme (1979) measured the ion leakage as total conductivity of a bathing solution to estimate the heat tolerance of plants using pieces of tomato lamina and epidermal strips of onion bulb. Onwueme placed the plant material in stoppered test tubes containing either de-ionised water or air, then immersed the tubes in a water bath set at the required temperature. The solute leakage method was used by Leopold, Musgrave and Williams (1981) to study the change of the membrane injury in response to leaf desiccation using leaf discs. A comparison between the conductivity and the vital staining method (the 2, 3, 5-triphenyl tetrazolium chloride reduction by the tissue) yielded a similar result (Chen, Shen & Li, 1982) and both were used to study adaptation of plants to high temperatures.

More recent studies of high temperature stress have attempted to distinguish the separate, irreversible changes which lead to tissue death (Björkman, Badger & Armond, 1980) including damage to cell membranes, photosystems and carboxylating enzymes. Such detail is, however, outside the scope of the present investigation.

7.2 Method

It was decided to use the solute leakage method to determine the leaf lethal temperature as it is convenient and gives an immediate result. As it may be difficult to decide how much leakage is lethal, observations on the vitality of the material were made for several days subsequently. For this purpose a group of *Citrullus* potted plants were grown in the growth cabinet (Controlled Environments, Canada, see Chapter 3) with photoperiod 14 hours and ambient temperature 30-32 °C.

For the experiment, fully expanded, mature leaves were selected. The leaves were cut off and their areas were measured using the leaf area meter. Then they were thoroughly washed with distilled water to remove any electrolyte adhering to the leaf surface as a result of cutting the petiole, watering and handling.

In each trial, 5 leaves were placed in 5 test tubes (18 x 155 mm hard glass) containing no water, and another 5 leaves were placed in tubes already containing distilled water (10 ml).

All the test tubes were thoroughly washed in advance with distilled water then with 2N HCl (to eliminate any ions adhering to the tube surface), and with distilled water afterwards. To expose the leaves to the required temperature the tubes were immersed in a covered waterbath set at the required temperature. Five minutes elapsed before the internal temperature of the test tube came into equilibrium with the external temperature as measured with the electronic thermometer (see Chapter 3 for its description). After 60 minutes at the specified temperature, the treatment ended, and in the case of the water immersion, the water was poured away. To assess damage to membranes, each leaf was then washed thoroughly while still in the test tube to eliminate any solutes on the leaf surface. Then an aliquot of distilled water was finally added to each test tube (10 ml) and the tubes were set aside for 10 minutes to allow for solute diffusion. After that, each tube was shaken for 1 minute and a sample of the solution was taken in a small plastic tube. Immediately, the plastic tubes were stored in the cold room until analysing their contents for potassium ions using the flame emission mode of the SP9 atomic absorption spectrophotometer.

After the treatment the leaves were transferred to petri-dishes containing moistened filter paper, and kept in the growth cabinet at an ambient temperature of 30-32 °C and a photon flux density of about 100 W m⁻² to observe any change in the leaf tissue in comparison with untreated ones. A scale was used to denote the change in the vitality of the leaves

daily. The leaf was considered to be dead if 50% of its colour changed from green to yellow or if it was obviously decomposed.

The experiment was run at a range of waterbath temperatures from 37- 55 °C in 3 °C steps, using a different set of leaves for each temperature. In a preliminary experiment the immersion method was used to expose the plant leaves to the same range of waterbath temperatures but in a time series: 5, 10, 15, 30 and 60 minutes. Survival of the leaves is reported.

7.3 Results

At the lowest temperature (37°C) the leaves survived for at least 8 days. However, even quite low temperatures ($40, 43^{\circ}\text{C}$) caused a reduction in this survival time and so presumably caused irreversible damage of some kind (Fig. 7.1). Survival time was greatly reduced following exposure at 46°C , and above 50°C survival was never more than 1 day. Clearly, it is impossible to define a sharp killing temperature, as, in the conditions of the experiment, all temperatures above 37°C cause damage that ultimately results in death. Whether the leaves were exposed in air or water had little or no effect on the outcome of the trial. Fig. 7.2 shows K^{+} leakage from leaves exposed to air along with the relation between the exposure temperature and the duration of leaves survival. Even the lower range of temperature influenced survival and, to a minute but measurable extent, K^{+} efflux. Analysis of variance showed significant difference between the treatments at $P = 0.01$ (Appendix D). It can be seen from the Figure that there is a sharp increase of K^{+} efflux at an ambient temperature of 49°C . The total leaf survival as a function of potassium leakage is plotted in Fig. 7.3. It is noteworthy that irrespective of how small is the amount of K^{+} leaked is, this nevertheless has an effect on the leaf survival afterwards.

Moreover, survival was greatly influenced by the duration of exposure. Exposure times less than 30 minutes hardly reduced survival when the temperature was below 50°C . When the exposure was as long as 60 minutes, survival was greatly reduced at 46°C (Fig. 7.4). Thus, there is a definite interaction between exposure time and exposure temperature.

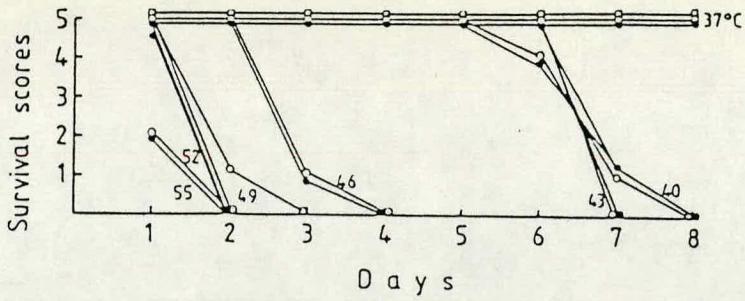


Fig. 7.1 Survival scores of leaves in air (open circle) or water (solid circle). Open squares denote control leaves at 33 °C in air. Maximum score (5) was given for leaves with no apparent damage at all. Exposure time was 60 minutes.

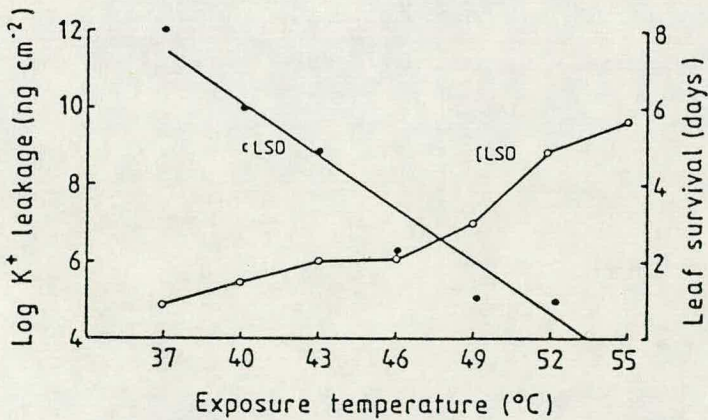


Fig. 7.2 Potassium ion K^+ leakage from the plant leaves at different air temperatures (open circle), solid circles represent the relationship between the exposure temperature and leaf total survival after the treatment ($r=0.9749$). Time of exposure was 60 minutes.

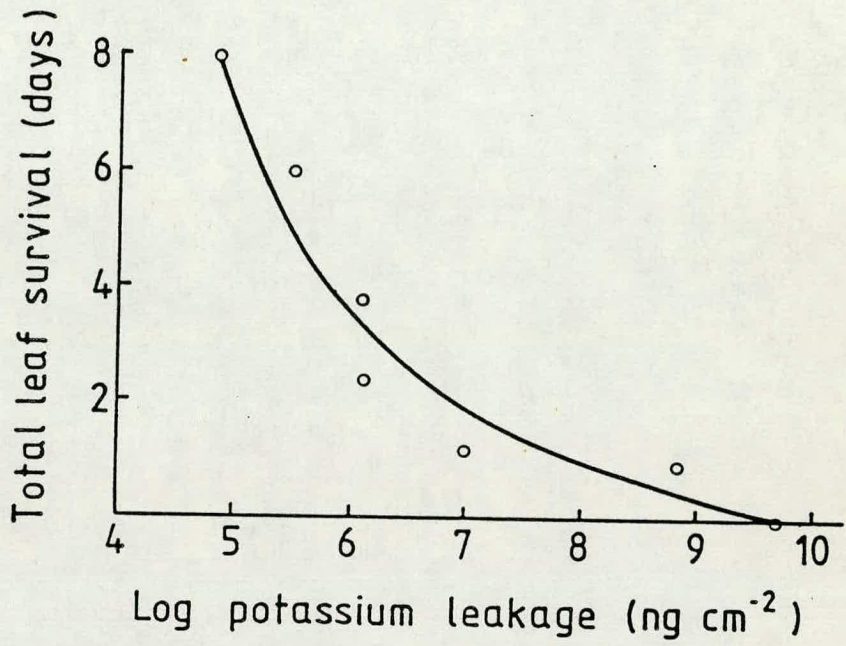


Fig. 7.3 Total leaf survival as a function of potassium leakage.

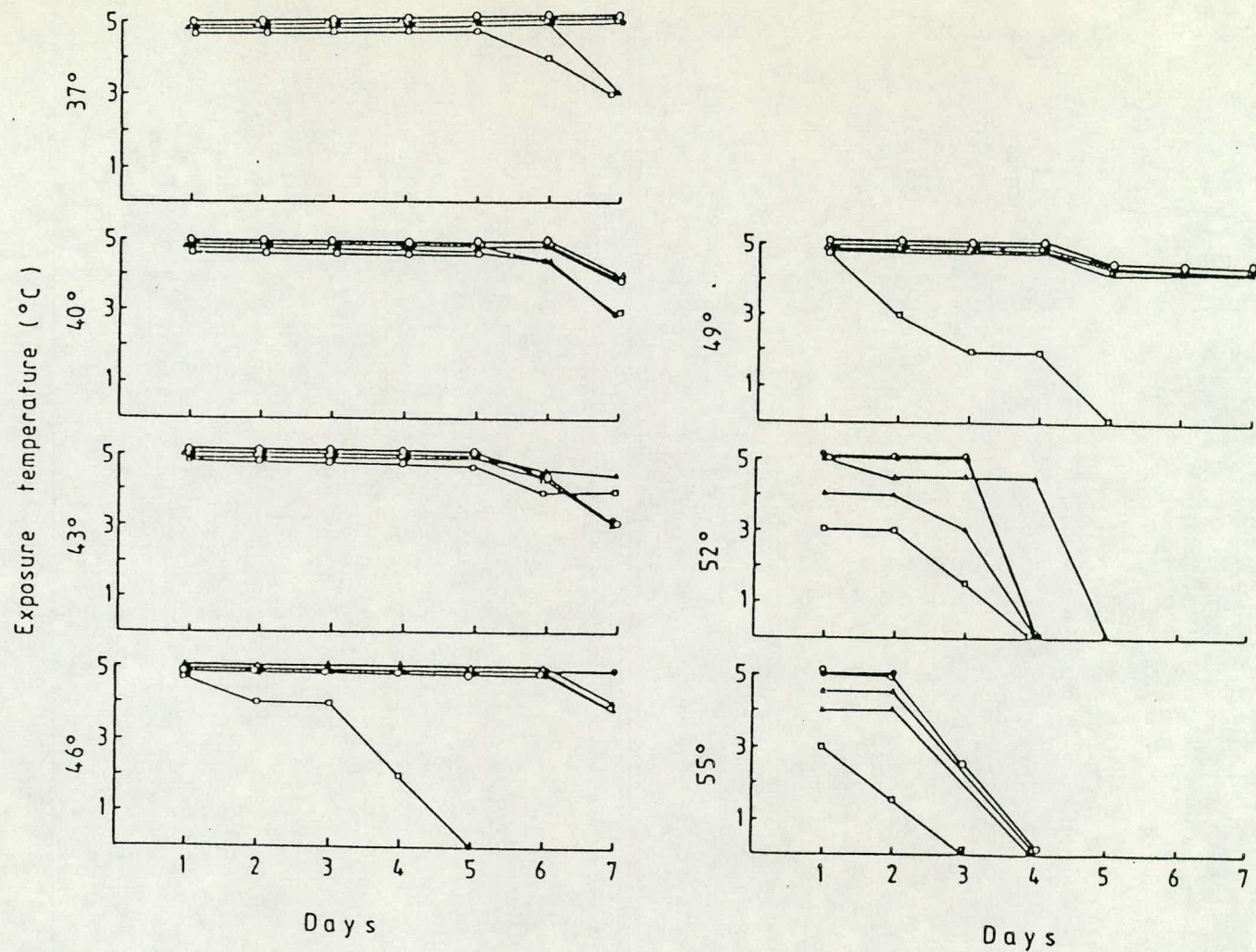


Fig. 7.4 The effect of the duration of exposure. Leaves were exposed by immersion in water for 5 minutes (O), 10 minutes (●), 15 minutes (Δ), 30 minutes (▲) and 60 minutes (□). The numbers from 1-5 on the ordinate axes denote the survival scores.

7.4 Discussion

Lange (1959) reported that plants were killed at lower temperature when they were immersed in water than when they were exposed to dry air. This was ascribed to the ability of plants to transpire and cool themselves if they are exposed to dry air. To reduce any transpirational cooling, only a detached leaf was used in the present experiment. Moreover, in the case of excised leaves, the effect of cytokinin in the root, which was reported to reduce the effect of high temperature on the shoot (Steponkus, 1981), was also eliminated. Thus the detached leaf does not experience any 'repair' process which might affect its ability to endure or recover after the exposure to a high temperature.

As reported by other workers who used the solute leakage method to assess the plant tissue injury, the potassium ion K^+ was the main solute leaking (Lieberman *et al.*, 1958; Patterson *et al.*, 1976). Presumably this merely reflects the high K^+ content of most plants. The solute leakage was found by some workers to be rapid in the first few minutes then followed by a linear rate (Leopold, Musgrave & Williams, 1981).

This rapid phase presumably is the loss of ions which have already leaked from cells and have become absorbed on the surface or, with the immersion method, are dissolved in superficial water.

A number of workers have used the Arrhenius plot to assess the effect of temperature on the change of state of the membrane. Simon (1974) pointed out that there was

serious controversy regarding the significance of the Arrhenius plot. For the present data, it was not possible to obtain the clear break in the line as expected from Arrhenius theory when the logarithm of the absolute temperature was plotted against the reciprocal of K^+ leaked. Probably this was due to the limited number of data points obtained from the experiment.

Interestingly, even a relatively low temperature ($<46^{\circ}\text{C}$) reduced the leaf survival with no apparent damage to the cell membrane being evident from the low amount of K^+ leaked (Fig. 7.2). Exposing the plant leaf to high temperatures ($>49^{\circ}\text{C}$) affected the leaf survival even when exposure was brief.

A sharp increase of K^+ leakage was measured at 49°C (Fig. 7.2) and a remarkable decrease in survival scores started at temperatures $>46^{\circ}\text{C}$. From this it can be said that temperatures around 49°C will normally cause serious damage to the leaf. In Lange (1959), *Citrullus* leaves were seriously damaged at 49°C when he used the immersion method and at 52°C in dry air. Thus the lethal temperature obtained in the present experiment for *Citrullus colocynthis* is rather low in comparison with Lange's result for dry air. However, Lange (1959) was exposing leaves that were still connected to the original plant and it could be that repair processes involving cytokinin were reducing the effect of the extreme temperature.

It should be noted that several vital processes may have to suffer damage before the leaf tissue is finally killed. Not all processes are damaged at the same temperature. Björkman

et al. (1980) reported inactivation of photosynthesis in the heat-adapted species *Tidestromia oblongifolia* at a temperature 5 °C below that required to kill the leaves. It appeared that the photosystems, rather than the overall photosynthetic system was disrupted. If this is generally the case, one might expect some interaction between temperature and light, with a high photon flux density imposing an additional strain on the photosystems. Leaf movements, to reduce the absorption of photon energy, might be very important in reducing such damage. It would be desirable to study photosynthesis in *Citrullus* from this point of view, establishing the effect of exposure temperature on rates of photosynthesis in plants acclimatized at different temperatures and investigating the role of photoinhibition at high temperatures.

In the desert, extreme temperatures occur for only a short time in the middle of the day. Information on the effect of temperature on survival suggests that leaf cooling is frequently necessary, in the hottest parts of the desert day when air temperature may exceed 50 °C. In many cases however, the 'cost' of water used in cooling is large, and so an optimum strategy would be to adopt a high rate of transpiration only as a last resort and then for only part of the day.

CHAPTER 8
FIELD MEASUREMENTS OF THE ENERGY BALANCE
OF *C. COLOCYNTHIS* LEAVES

It was reported in chapter 1 that plants growing in environments in which high temperature is accompanied by high radiant energy must have adaptive features to dissipate excessive heat. These plants may gain access to water by having deep and efficient root systems to tap subterranean supplies, this holds true in *Citrullus* as was shown in chapter 6, or may have a distribution restricted to places where surface water is ample. This group of plants can dissipate heat by maximising the latent heat loss and thus keeping the leaf temperature below the lethal point and below air temperature through having high stomatal conductance and combining that with reducing the sensible heat gain by possessing a relatively large leaf with a correspondingly low boundary layer conductance (Grace, 1983; Jones, 1983).

When water is severely limited, plants have to adopt a different strategy: a small leaf with high boundary layer conductance seems to be a widespread evolutionary development to increase the heat loss by losing the sensible heat to the ambient air and thus avoiding over-heating (Campbell, 1977; Gates, 1980; Jones, 1983). Leaves of such plants are commonly at nearly the same temperature as the air.

It was shown in chapter 3 that *C. colocynthis*, when well watered, displays a very high stomatal conductance, g_s , in

comparison with other desert plants. Those values were obtained for watered plants in laboratory conditions whereas in nature the plant is not obviously so well supplied with water. Therefore field measurements of leaf conductances on well-established plants are of interest to give some idea of how plants survive the dry, hot season. Another reason for studying the species in its natural environment is to obtain a suitably wide range of radiant energy loads, difficult to achieve in laboratory conditions. Thus, determinations of leaf conductances g_s and g_a were made, along with determinations of transpiration rate E , in the field at the end of summer 1983 on plants growing *in situ* at three sites chosen to cover much of the range of the species in Saudi Arabia.

8.1 Stomatal conductance g_s in desert plants (background)

Although there is insufficient information in the literature about the stomatal and boundary layer conductances of desert plants, it is at least established that many species have a very low stomatal conductance whilst others have a relatively high g_s (as shown in Table 1.1).

Stomatal closure in the day time is a common phenomenon among the succulent plants in hot dry environments (Meidner & Mansfield, 1968; Schulze & Hall, 1982; Willmer, 1983). This complete or partial closure causes those plants to have a very low g_s . Stomatal response to the conditions in the desert has been of concern to investigators working in Negev Desert in the last decade. Under dry atmospheric conditions stomata

close in some species resulting in low stomatal conductance g_s , while under humid ambient air those plants have a high g_s (Schulze et al., 1972; Lange et al., 1975). At low water stress, some desert plants showed an increase in stomatal conductance as the leaf temperature was increased while at high water stress they had a reverse response with the temperature increasing (Schulze et al., 1973). The authors reported this pattern of stomatal response for four native species of the Negev Desert: *Zygophyllum dumosum*, *Artemisia herba-alba*, *Hammada scoparia* and *Reaumuria negevensis*.

Under dry conditions, some plants have a high stomatal conductance only in the beginning of the day whereas others have high g_s in the early morning and late afternoon. Schulze and Hall (1982) discussed these kinds of stomatal responses of arid region plants. They ascribed the opening of the stomata in the morning to the low vapour pressure deficit while the low g_s at midday was caused by the stomata closure at high temperature and high leaf to air vapour pressure difference.

In field measurements of stomatal conductance of *Phragmites communis* in Death Valley, the maximum value of g_s was recorded in the early morning and it has remained as it is until evening (Pearcy et al., 1974). A sharp increase in the stomatal conductance to water vapour just after illumination was reported by Smith and Nobel (1977b) for the broad leaved desert shrub *Hyptis emoryi*. After the high g_s in the morning a partial stomatal closure occurred, leading to a low stomatal conductance for the rest of the day. Pearcy and Harrison (1974) reported a maximum g_s exhibited by *Atriplex lentiformis*

during midday when solar radiation is at its highest. Also a low stomatal conductance g_s was measured early and late on a dry Summer day for *Arbutus unedo* (Portugal) by Tenhunen *et al.* (1980).

8.2 The experimental sites and their microclimate

The Arabian Peninsula consists mostly of sandy deserts classified by Stocker (1976) as absolute deserts with a continental climate. The maximum rainfall occurs in the winter with no regular pattern in each year. In the largest extreme arid desert, Rub'al Khali in the south of Saudi Arabia, drought can last for years.

The ground water in the Peninsula is, however, quite abundant with a minimum depth of 90-200 m in the east. Its depth increases from the east to the west (Petrov, 1976). The surface water is scarce though just below the ground surface in the wadis which are an important element of the desert topography of the Arabian Peninsula, supporting vegetation even in the dry season.

Field measurements were conducted for 3 days in three different places thought to be different in their microclimate. These were Dammam on the east coast (Long. $50^{\circ} 05''$ E. Lat. $26^{\circ} 24''$ N. and elevation 5 m), Nuayriyah (Long. $48^{\circ} 28''$ E. Lat. $27^{\circ} 28''$ N. with an elevation of 50 m), and Riyadh, Wadi Huniffa, (Long. $46^{\circ} 49''$ E. Lat. $24^{\circ} 40''$ N. and elevation 610 m). They are shown in Fig. 8.1. These will be referred to as the coastal, desert and wadi site respectively. The average

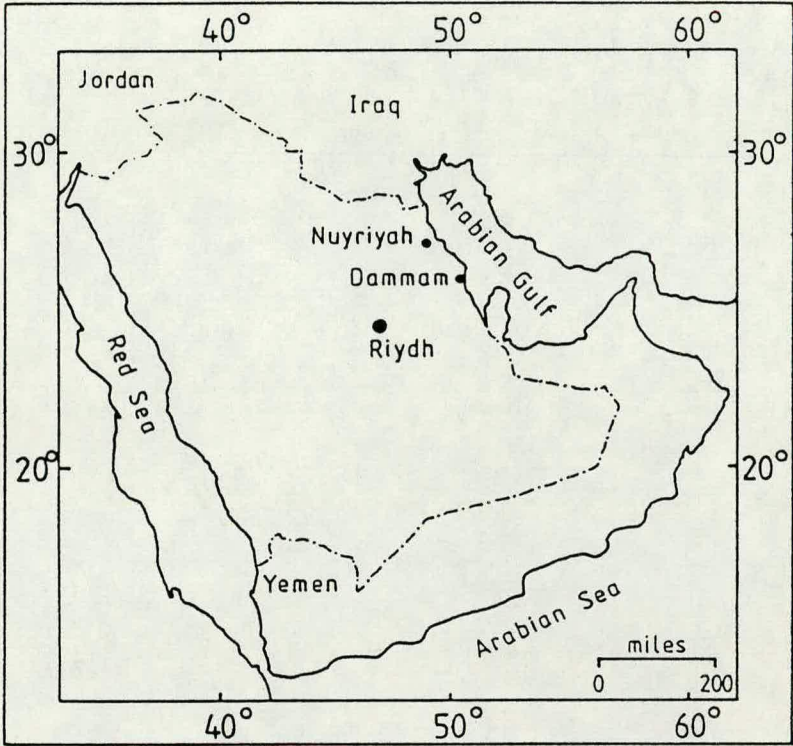


Fig. 8.1 A map of the kingdom of Saudi Arabia to show the experimental sites.

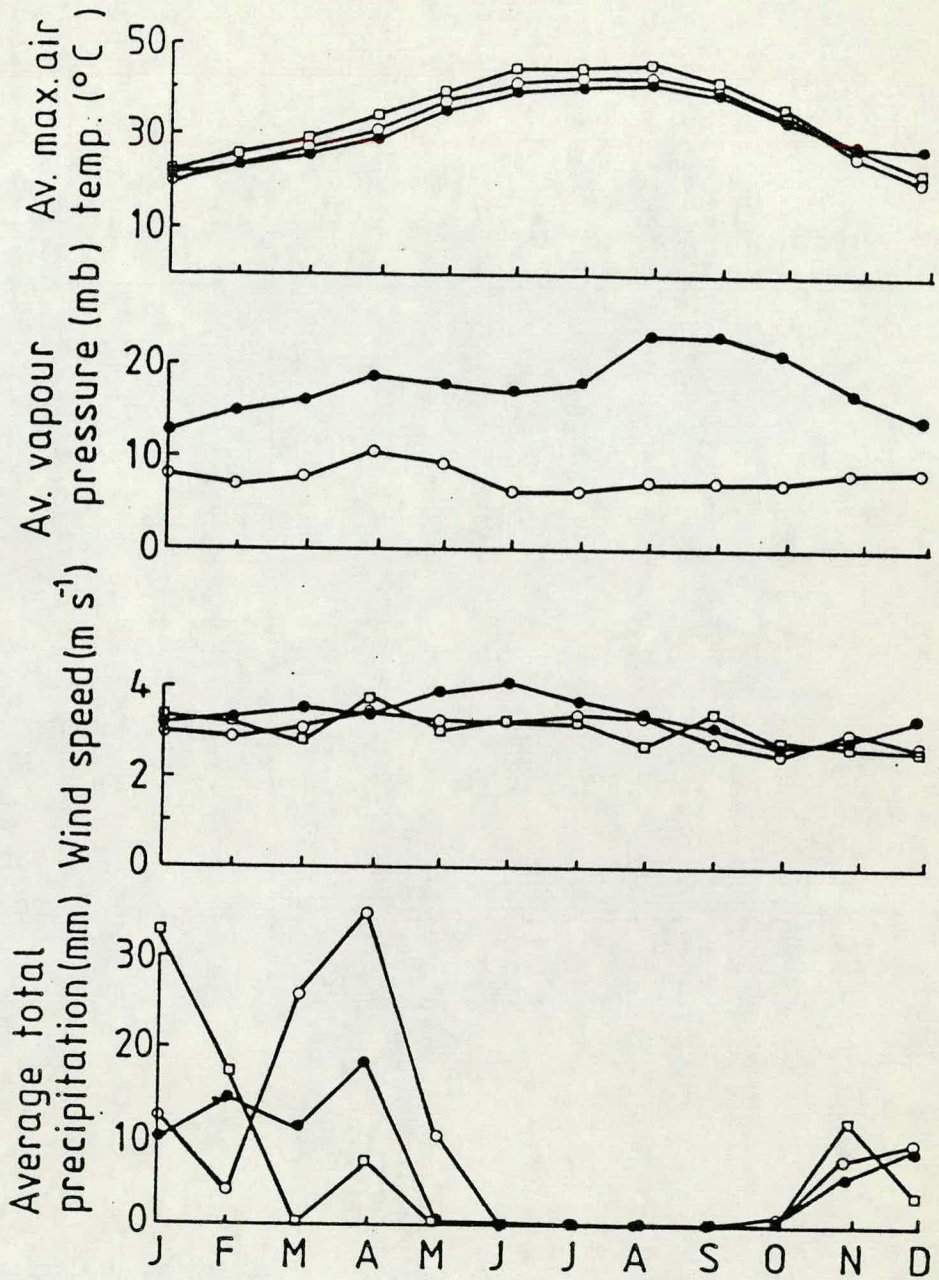


Fig. 8.2 Climatological data for the experimental sites for the Coast (solid circle), wadi site (open circle) between 1960-1976 and desert site (open squares) between 1960-1976. No data on water vapour pressure was available from the desert site. Data were recorded at the nearest meteorological station, Dhahran, Riyadh and Nuayriyah for coast, wadi and desert respectively. Each station is within 6-10 miles of each site (After Agro-climatological Study in the Arab Countries, Saudi, 1977).

climate of the experimental sites is shown in Fig. 8.2. They all display high temperature in the summer with no rain. Wind speed is quite high throughout the year, especially in the summer.

8.3 Methods

The measurements were carried out on 26-28 September 1983 and 2 October 1983 at the coastal, desert and wadi sites respectively. The techniques were broadly the same as those outlined previously in chapter 3. It was found more convenient to use cardboard models as non-transpiring leaves rather than to use vaselined leaves. *C. colocynthis* cardboard leaf models were shaped as described in chapter 4 and painted green.

For the measurements of surface temperature, two sets of copper-constantan thermocouples (42 SWG) were constructed, each set consisting of 3 junctions connected in parallel with a fourth one as the reference.

By September, the plants consisted of large mats with many stems. Only healthy, densely growing plants were chosen for the measurements. Surface temperature of transpiring leaves T_L and non-transpiring leaves T_L^* were sensed by attaching the three thermocouple junctions to the abaxial surface of 3 representative leaves using Sellotape glue, and to the lower surface of the cardboard models, and both thermocouple sets were referenced to the dry bulb of the psychrometer unit. Models were positioned within the plant canopy and precautions were taken to keep them away from the ground. Only the leaf model 'petiole' was permitted to

touch the neighbouring leaf. The model's posture was adjusted to resemble that of the transpiring leaves.

The shortwave flux was sensed by a quantum sensor (T & J Crump Scientific Products, Essex). The dry and wet bulb temperatures were measured using an aspirated, double shielded, tube psychrometer. All sensors were mounted 20-30 cm above the ground. Their signals were scanned every 10 s and integrated over each half-hour period using a data logger (CR21 Micrologger, Campbell Scientific Inc., Utah, U.S.A.).

It was possible in the wadi site to measure, in addition, the wind speed near the plant with a cup anemometer.

Plate 8.1 shows the equipment being operated in one experimental site (wadi).

8.3.1 The net radiation R_n estimation

The net radiation R_n absorbed by both leaf and the cardboard model is estimated by converting the downward photon flux (PAR) to the shortwave energy flux ($W\ m^{-2}$) by dividing it by an appropriate conversion factor (4.6) (McCree, 1981). It was further assumed that the near IR component was equal to this PAR shortwave component (Szeicz, 1974). The absorptance of the solar radiation was estimated using the data from chapter 4.

The downward longwave flux was calculated by using the Swinbank formula for clear sky longwave radiation (Monteith, 1973) as follows:

$$L_d = 1.20 \sigma T_a^4 - 171$$



Plate 8.1 The equipment being operated in the wadi site.

where L_d = the downward longwave flux

σ = Stefan-Boltzmann constant ($5.67 \times 10^{-8} \text{ W m}^{-2} \text{ K}^{-4}$)

T_a = the air temperature in degrees Kelvin

By applying the Stefan-Boltzmann law, the outgoing longwave radiation from the leaf and the cardboard model can be calculated as was shown in chapter 2. Since the absorption of the plant leaf and the leaf model are known (Table 4.3.1), that enabled us to estimate R_n absorbed by both the leaf and the model.

8.3.2 The aspirated tube psychrometer

The air temperature and wet bulb depression were measured by using two thermistor sensors. The sensor type was chosen to be compatible with the CR21 micrologger, enabling the use of its built-in program to interpret the signal. The thermistors were embedded at the tip of 1 ml plastic syringes and mounted vertically in a double shielded device. This psychrometer unit is referred to as the aspirated tube throughout this text. It was constructed especially for the field measurements, bearing in mind the necessity of small size to facilitate transport. A transverse section of the aspirated tube psychrometer is shown in Fig. 8.3. It consists of external PVC tube 5 mm thick (50 mm diameter, 155 mm length) and internal brass tube 1 mm thick (36 mm diameter, 150 mm length). Both tubes were covered with aluminized

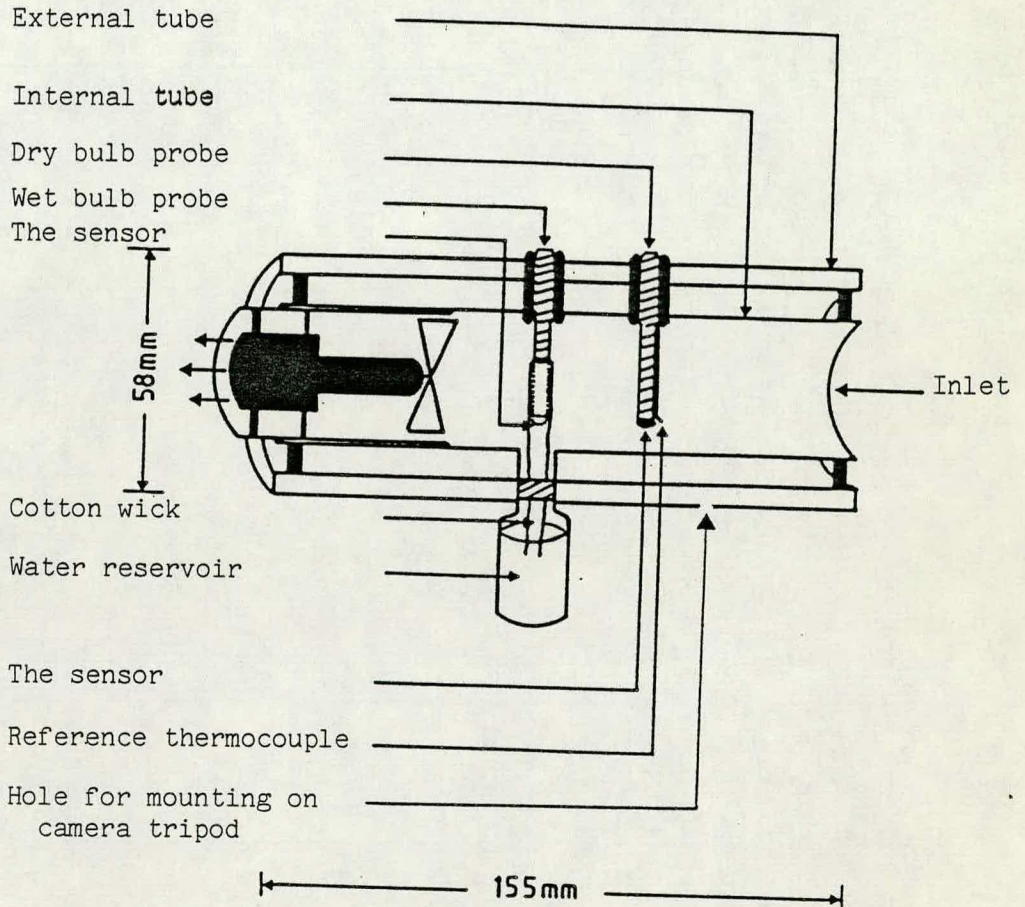


Fig. 8.3 A transverse section of the aspirated tube psychrometer.

Mylar, self-adhesive 'Melinex' chosen for its high reflectance in shortwave and its high emissivity in the longwave. For ventilation of the internal tube a fan was employed (Micronel D.C. miniature fan, Model V361L). Maximum wind speed produced by it, found with a hot-wire anemometer replacing the wet bulb thermistor, was 2 m s^{-1} when a 6 volt supply was applied. A plastic bottle holding 13 ml of distilled water was used as the water reservoir (the reservoir need refilling about twice each day).

8.3.3 The calibration of the sensors and the leaf model readings

A calibration of the aspirated tube against the Assman psychrometer was done in the Fisons growth cabinet (Model 2340) at different air water vapour pressures and at an ambient air temperature of 35°C . A range of voltages were applied to the fan within the aspirated tube to explore the effect of fan speed (Table 8.1). The discrepancy between the wet bulb readings of the Assman psychrometer and the home-made psychrometer unit could not be attributed to poor ventilation but could be attributed to heat transfer between the wet bulb and the dry part of the sensor and tube. It is similar qualitatively to the discrepancy found in some commercial units (e.g. Psychrometer, Delta-T, Cambridge). In a later design used in our laboratory (Allen, Wilson & Grace, unpublished) the problem is overcome by using probes that are very long in relation to their diameter. However, in the present work the discrepancy was only discovered

Air vapour pressure (mbar)		Fan power (volts)					
		0	3	6	9	10	
42.4	1	D	36.6	35.4	34.7	34.4	34.3
		W	33.4	32.4	32.2	32.1	31.9
		Δ	3.2	3.0	2.5	2.3	2.4
	2	D			34.5		
		W			30.7		
		Δ			3.8		
37.8	1	D	37.3	35.3	34.6	34.5	34.4
		W	33.1	30.9	30.8	30.9	30.8
		Δ	4.2	4.4	3.8	3.6	3.6
	2	D			34.5		
		W			29.4		
		Δ			5.1		
17.7	1	D	37.7	35.5	34.7	34.4	34.4
		W	29.4	25.0	24.8	24.6	24.6
		Δ	8.3	10.5	9.9	9.8	9.8
	2	D			34.7		
		W			21.7		
		Δ			13.0		
10.2	1	D	37.7	35.6	34.6	34.4	34.5
		W	28.1	21.9	21.7	21.5	21.5
		Δ	9.6	13.7	12.9	12.9	13.0
	2	D			34.7		
		W			17.8		
		Δ			16.8		

where 1 = the aspirated tube psychrometer
 2 = Assmann psychrometer
 D = the dry bulb temperature
 W = the wet bulb temperature
 Δ = the difference between the dry bulb and the wet temperature

TABLE 8.1: A comparison of the wet bulb depression between the aspirated tube and Assmann psychrometer at different air vapour pressures and at ambient temperature 35 °C. Radiation load on the instruments was about 500 W m⁻².

retrospectively, and the field data were corrected by using the relationship in Fig. 8.4.

The thermistors were calibrated against the precision electronic thermometer capable of resolving 0.01°C (Model No. 9335, Guildline Instruments Ltd. Canada) the results are shown in Fig. 8.5. This performance of the thermistors, with the CR21 program, is consistent with the specification given in the Campbell Scientific Instruments data sheet.

Two Crump quantum sensors were calibrated against a Li-Cor quantum sensor fixed to the LI-1600 porometer (Model Quantum, Sr. No. Q4955). The relation between the 'best' Crump sensor and the Li-Cor sensor is plotted in Fig. 8.6. There were substantial differences between the makers' calibration in the case of the 'worst' Crump sensor: such differences can only be caused by poor calibration practice by the maker, as the sensors were new. Only data from the 'best' sensor are reported, and the Li-Cor was assumed to be correct.

It was found that there was a difference between the temperature of the upper and lower surface of the cardboard when they were measured by attaching the two thermocouple junctions to both surfaces. This difference was dependent on radiation flux (Fig. 8.7). From Fig. 8.7 it is possible to infer an 'average' model temperature at any stated temperature excess and radiation load.

All these corrections were applied to the raw data before the calculations of resistances were made.

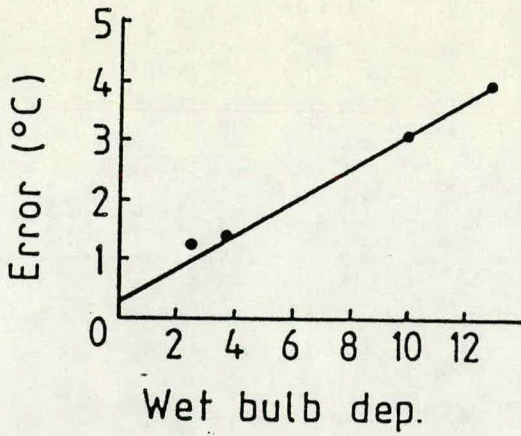


Fig. 8.4 The error in the measured wet bulb depression in the range 0-30 °C. The slope of the line is about 0.29.

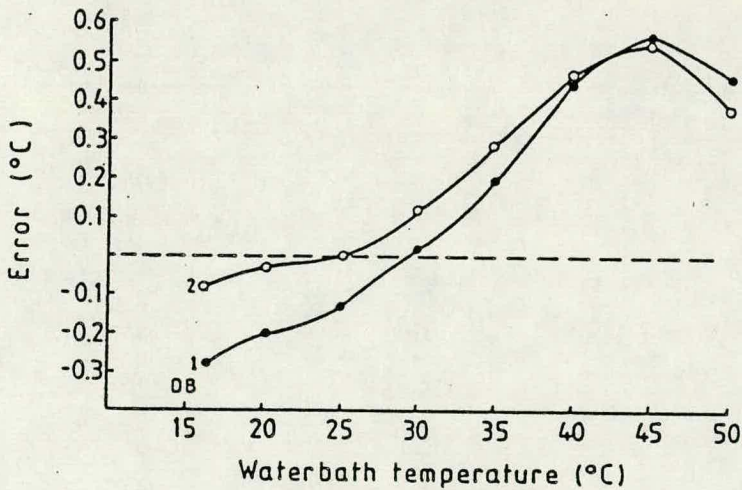


Fig. 8.5 Comparison between the thermistors and a precision thermometer output when they were immersed in a waterbath at a range of temperatures. Solid circles represent thermistor 1 and open circles represent thermistor 2. These were later used for sensing the dry and wet bulb temperatures respectively. The dotted line is the precision electronic thermometer output which was used as the standard.

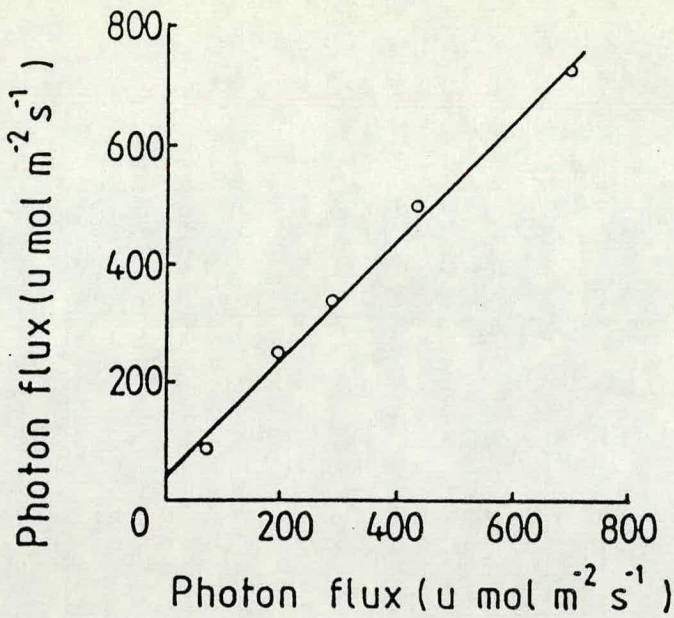


Fig. 8.6 A plotting of the quantum sensors (the abscissa axis) against Li-Cor quantum sensor (the ordinate axis). The slope of the line is 0.994.

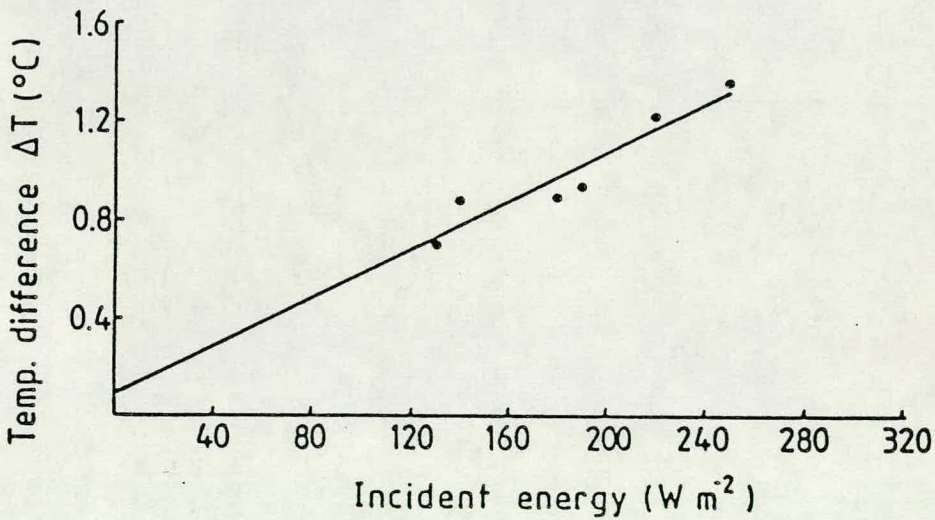


Fig. 8.7 The difference between the upper-lower surface temperature of the cardboard model at different levels of incident light energy as measured in the growth cabinet. The slope is $0.0048 \text{ } ^\circ\text{C}/\text{W m}^{-2}$.

8.3.4 Error analysis

Errors are unavoidable with any measuring system particularly in field measurements (e.g. Woodward & Sheehy, 1983). Estimating the net radiation R_n in the early and late part of the day when energy fluxes are very low might be the most serious in the present work. Errors can be evaluated from a knowledge of calibration data and from a familiarity with procedure. Statistical (sampling) errors as well as instrument errors might occur. Moreover, in calculations that involve several measured variables, the scope for maximum error must be considered. However, maximum errors, when all sources of error work in the same direction, are unlikely to happen, except in a few cases. Instead of estimating these maximum errors, it is possible to estimate probable errors. As described by Fritschen and Gay (1979) probable errors were estimated by a numerical procedure, incrementing each measured variable in turn within limits defined as the maximum error considered possible for each variable. The calculation of transpiration rates and conductances was then made for every possible combination of errors, by recalculating several thousand times. The new value each time was put in frequency classes to produce a frequency distribution covering the several thousand trials. Finally, the central $2/3$ of the results are taken to define the likely band of error, using the argument that the extremely high $1/6$ and extremely low $1/6$ of all trials are unlikely to occur in practice. In practice the value of this procedure depends on honest estimation of maximum errors in the individual variables in the first place.

Assumed errors for each are as follows:

Variable	Estimated error about the measured value	Increment step
Rn	$\pm 15\%$	0.05
T _a *	$\pm 0.6^{\circ}\text{C}$	0.2
T _L	$-0.5 - +0.9^{\circ}\text{C}$	0.2
T _L	$\pm 0.6^{\circ}\text{C}$	0.2
WBD	$\pm 15\%$	0.05

A computer program was used to do these calculations (Appendix E). Some 6,000 iterations are required in each error estimation, and so the procedure is somewhat extravagant in computer time.

8.4 The results

At the three sites *C. colocynthis* leaf temperature T_L was either slightly above or below the air temperature T_a as shown in Fig. 8.8b; 8.9b and 8.10b. However, T_a during the experimental days did not exceed 40°C . Maximum solar energy was measured at the wadi site at solar noon (Fig. 8.10a). In the desert site the highest wet bulb depression (WBD) was measured: for much of the day it was 20°C (Fig. 8.9b).

The partitioning of absorbed energy as sensible heat and evaporation λE is plotted in Fig. 8.11. The sign convention (C) is that heat losses from the leaf to the air are negative.

The plant stomatal conductance g_s , transpiration rate E and the boundary layer conductance g_a for the three sites are shown in Fig. 8.12, 8.13 and 8.14 for the coast, desert and wadi sites respectively. Maximum g_s occurred at all sites in the beginning of the day. It decreased gradually as the day progressed reaching a minimum value at late afternoon. Maximum stomatal conductance was measured in the coast site (0.0072 m s^{-1}).

The trends of the transpiration rate were about the same in all experimental days, having relatively low E in the morning and maximum values in the middle of the day, after which E decreased reaching a minimum at the end of the day except in the desert site when the early morning value of E was higher than that at other sites (Fig. 8.12b). The maximum E was $0.19 \text{ g m}^{-2}\text{s}^{-1}$ at the middle of the day in the desert site.

The pattern of the boundary layer conductance was not

the same in the three sites. In the coastal site g_a was around 0.05 m s^{-1} most of the day while in the desert, a maximum g_a was in the early morning after which it gradually declined reaching its minimum at midday. In the wadi, maximum g_a was measured just before late afternoon (0.089 m s^{-1}). These trends presumably depend on the daily pattern of wind speeds, with perhaps some influence of wind direction.

The wind speed (u) in the wadi site (the only case where measurements were possible because the anemometer was borrowed specially that day from the King Saud University) during the course of the day are shown in Fig. 8.15. The wind speed increased as the day progressed and the relationship between g_a and u for the wadi site are plotted in Fig. 8.16.

The relationship between stomatal conductance and leaf-air VPD for the three sites are plotted in Fig. 8.17. There is only a weak indication of a relationship between g_s and VPD. Fig. 8.18 shows the transpiration rate plotted together with the incident solar energy at the three experimental sites.

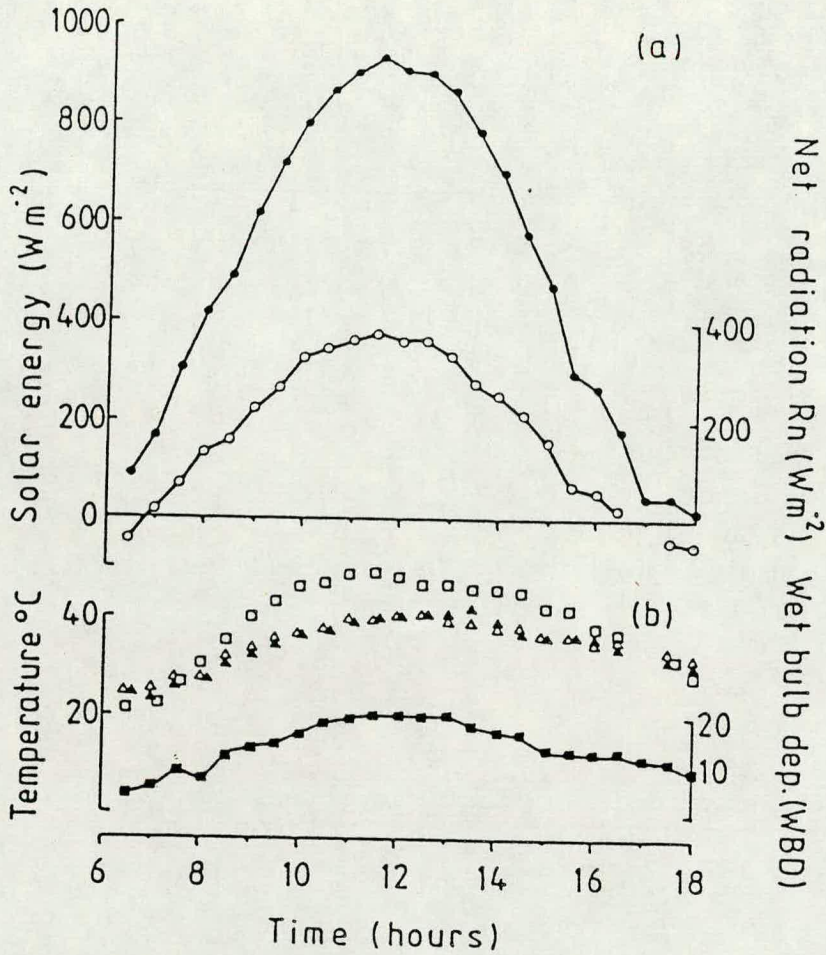


Fig. 8.8 a) The solar radiation flux during measurements at the coastal site (●—●) and the net radiation R_n (○—○) absorbed by the plant leaf;

b) The air temperature (Δ), real leaf (\blacktriangle) and the leaf model (\square) temperatures. \blacksquare — \blacksquare denotes the wet bulb depression (WBD).

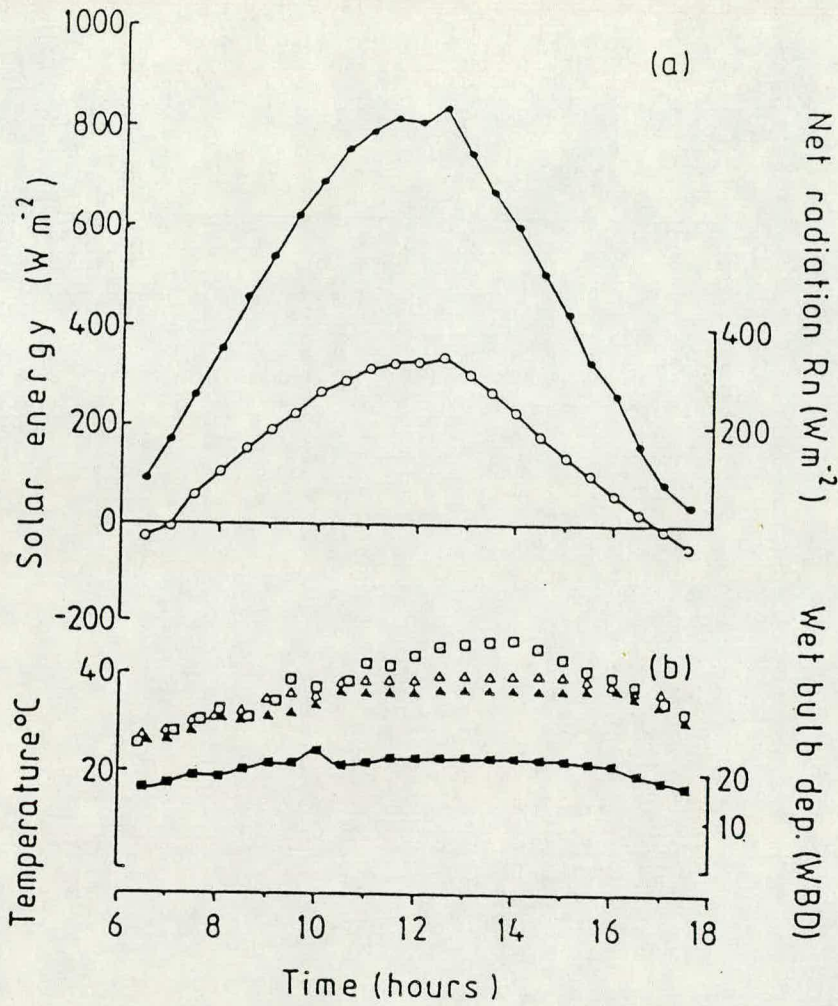


Fig. 8.9 a) The solar radiation flux during measurements at the desert site (●—●) and the net radiation R_n absorbed by the plant leaf (○—○);

b) The air temperature (Δ), the leaf (\blacktriangle) and the leaf model (\square) temperatures. —■— the wet bulb depression (WBD).

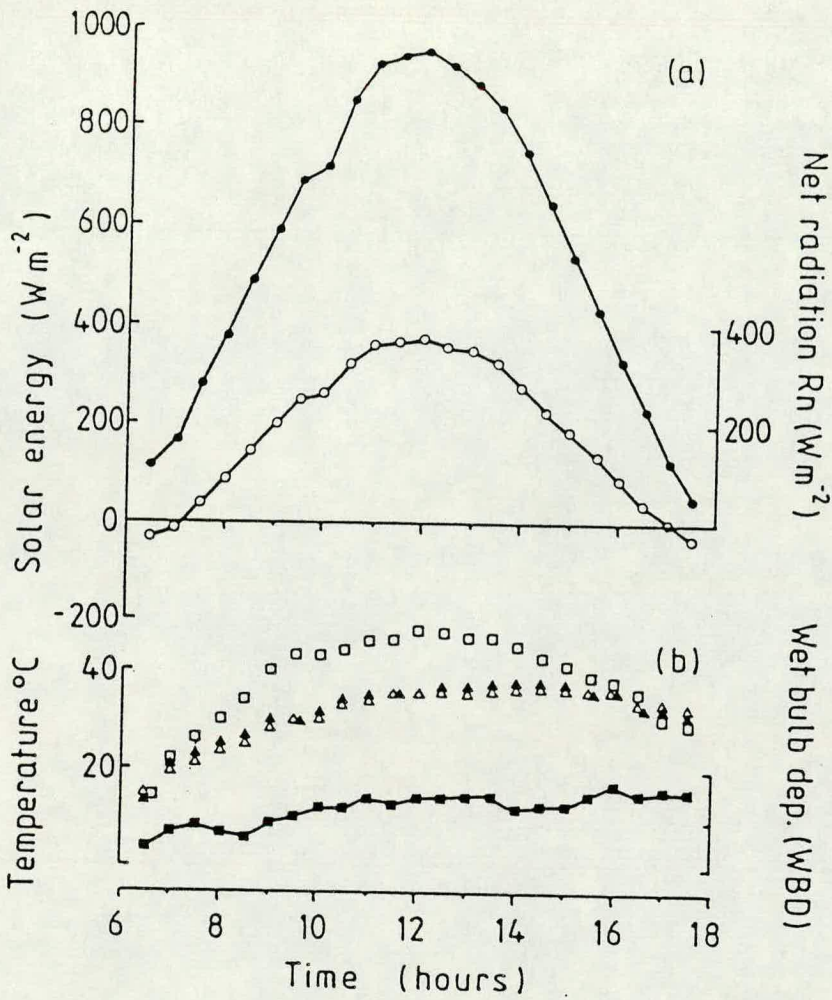


Fig. 8.10 a) The solar radiation flux (○—○) and the net radiation (●—●) absorbed by the plant leaf at the wadi site;

b) The temperature of the air (Δ), leaf temperature (\blacktriangle) and the cardboard model temperature (\square). \blacksquare — \blacksquare denote the wet bulb depression (WBD).

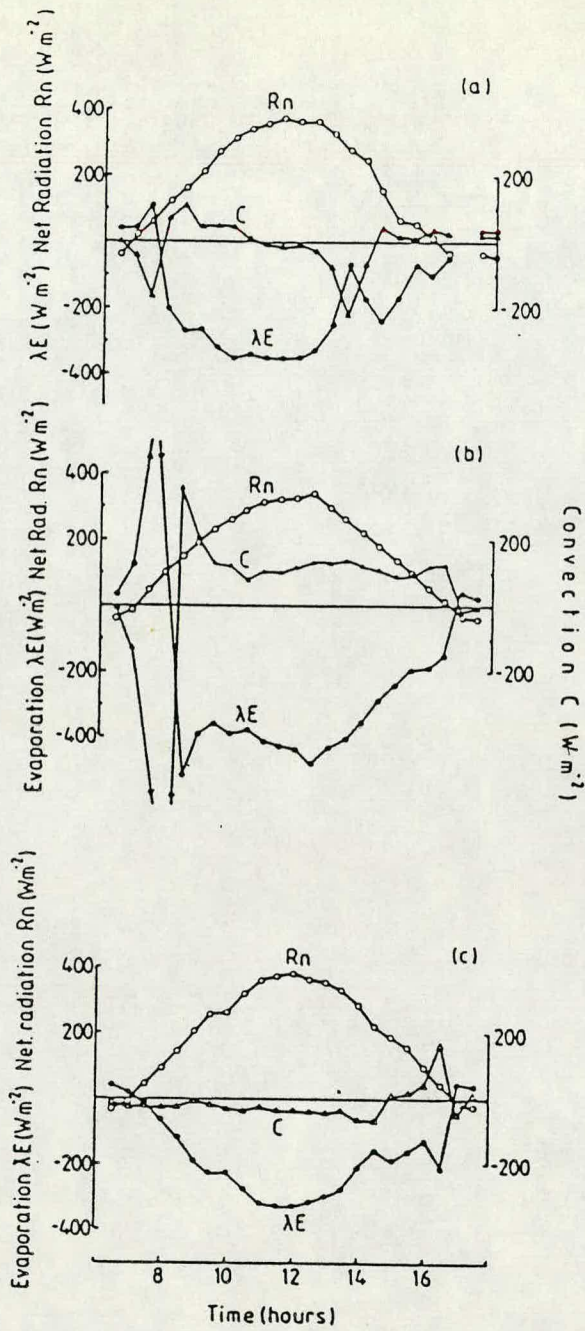


Fig. 8.11 The partitioning of the absorbed energy between the evaporation λE and convection C . In the coast (a), desert (b) and the wadi site (c).

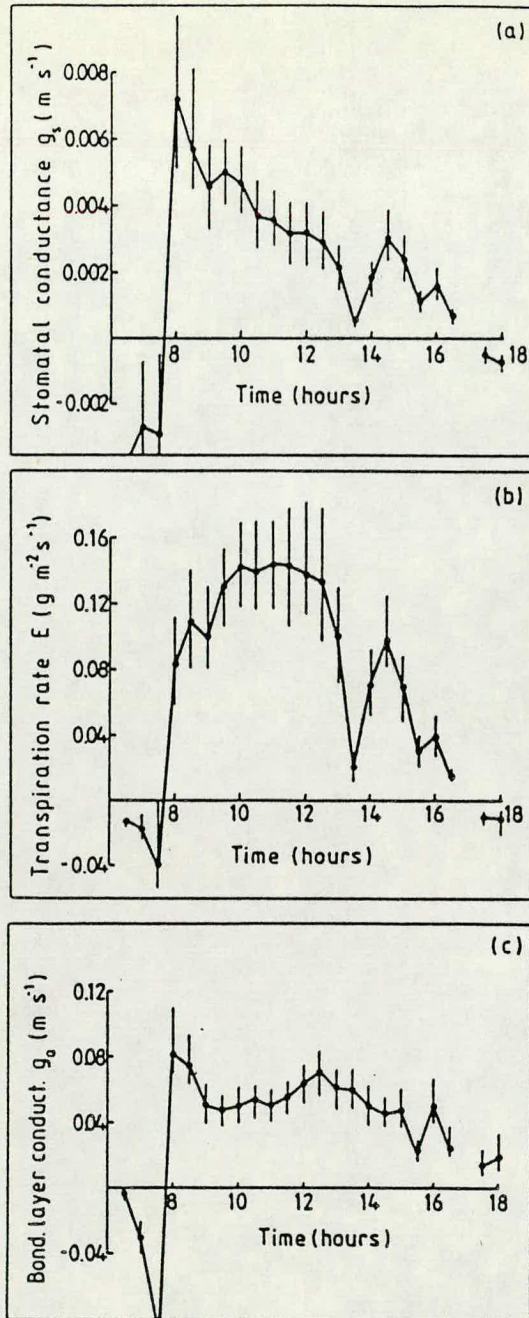


Fig. 8.12 The diurnal trend in stomatal conductance g_s (a), the transpiration rate E (b) and the boundary layer conductance g_a (c) at the coast site. The error bars show the maximum and minimum probable error at each reading. (Data at 17.00 are omitted due to uncertainty.)

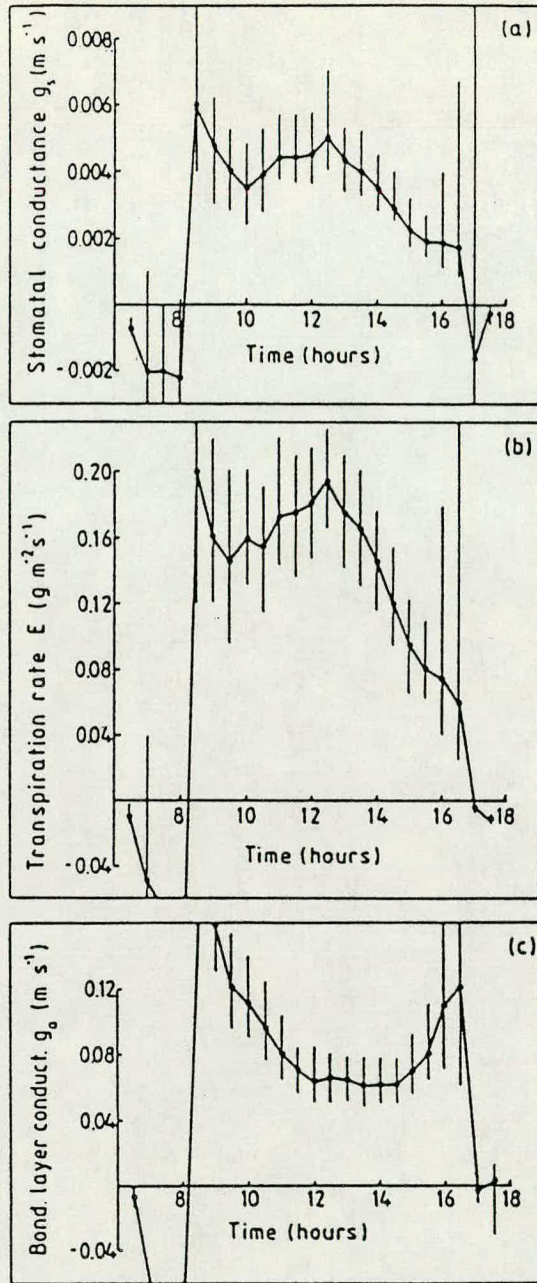


Fig. 8.13 The stomatal conductance g_s (a), transpiration rate E (b) and the boundary layer conductance g_a (c) during the desert measurements day.

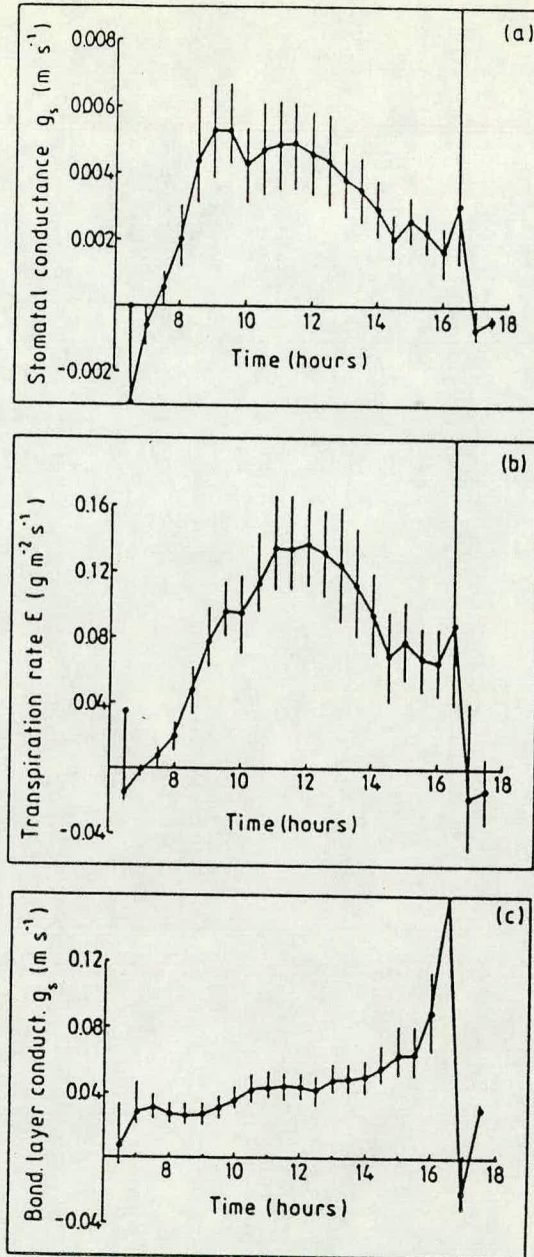


Fig. 8.14 Daily measurements of g_s (a), E (b) and g_a (c) at the wadi.

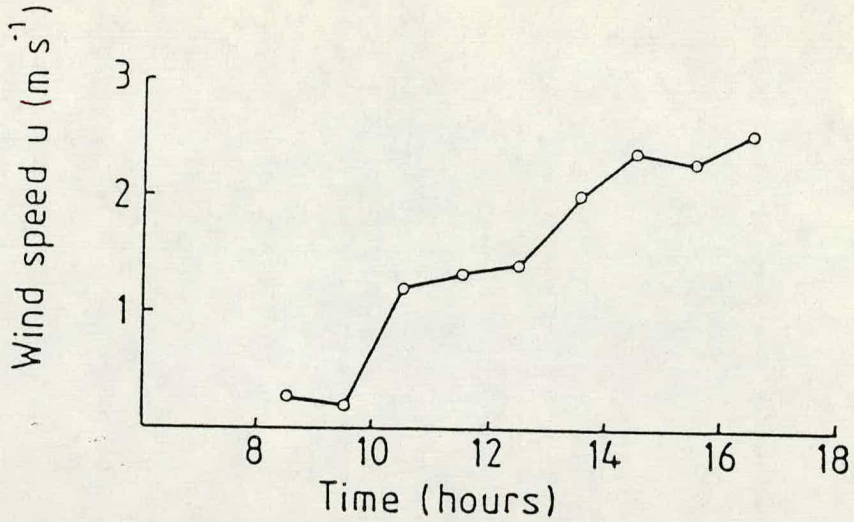


Fig. 8.15 Wind speed in the wadi during the course of measurements day. Data are mean values for each hour of the day.

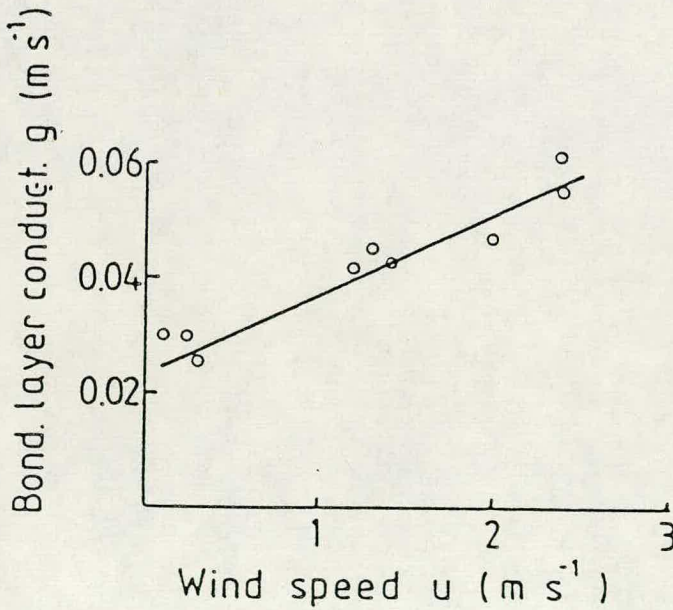


Fig. 8.16 The relationship of g_a and the measured wind speed 20 cm above the ground in the wadi site during the course of the day. The g_a estimate at 16.30 is omitted as its value is uncertain (See Fig. 8.13c).
 $r = 0.9558$

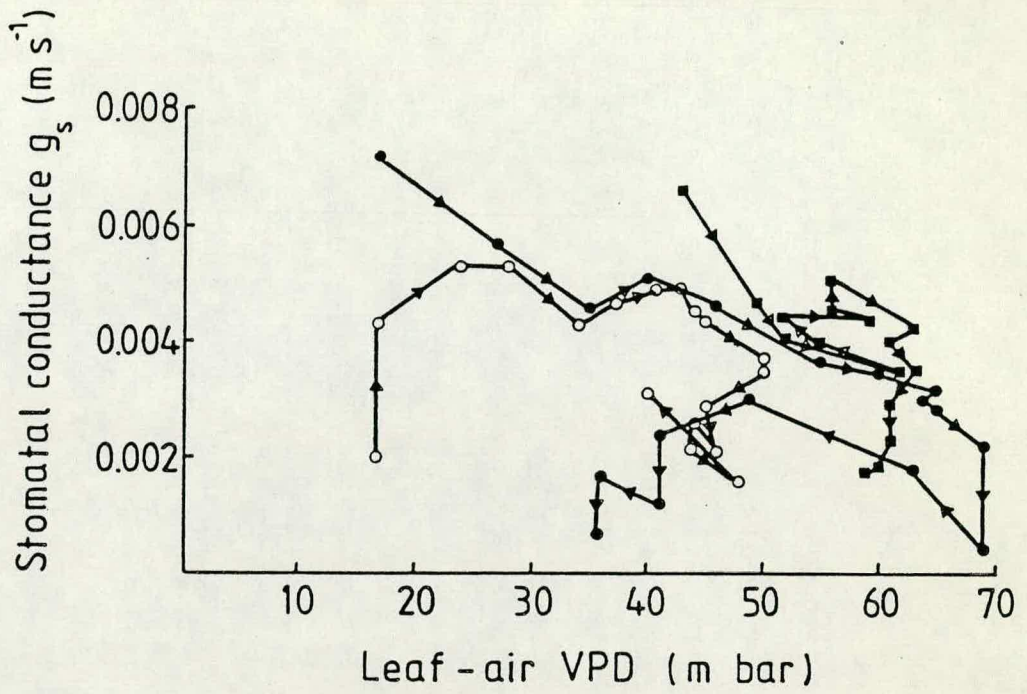


Fig. 8.17 The relationship between the stomatal conductance and leaf-air VPD in the coast (●), desert (■) and the wadi site (○) during the three experimental days. Arrows show the sequence during the day. Only the 'respectable' values of g_s were plotted.

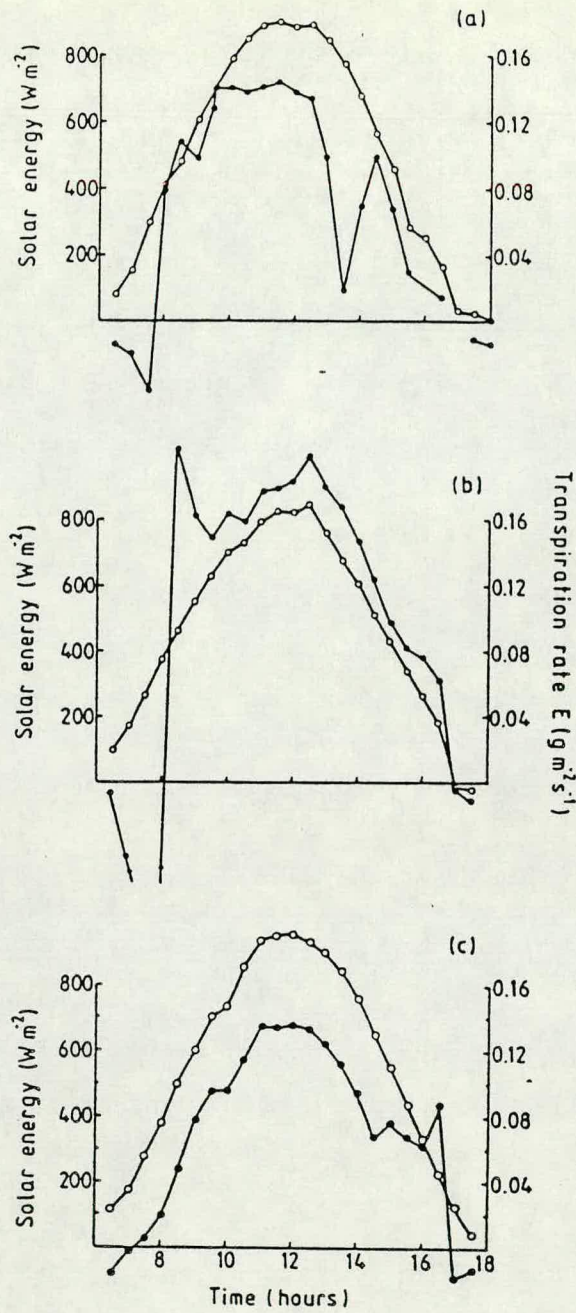


Fig. 8.18 Plotting of transpiration rate E (solid circle) and the solar energy flux (open circle) for the three experimental days; at the coast (a), desert (b) and wadi site (c).

8.5 Discussion

It was thought that the technique of using a cardboard model as a non-transpiring leaf was of some practical advantage; mainly to solve the problem that sometimes occurs with the method otherwise: the complete prevention of transpiration from a leaf is surprisingly difficult with rough leaves such as *C. colocynthis*. Other problems with vaselined leaves which can be encountered when working outdoors in the desert include the possibility of the moving sand or dust sticking on the petroleum jelly. Furthermore the cardboard is flexible and it is easy to match its posture to that of the transpiring leaf in such a way that the model receives the same amount of the incident radiation especially when the transpiring leaf undergoes leaf movements. The major disadvantage, as discussed elsewhere, is that the near infrared absorptance of the model is a very poor match to that of the leaf, so that the calculations require further data, on the optical properties of the leaves and models, and they are not as straightforward as otherwise.

It was shown in chapter 3 how *C. colocynthis* leaf temperature can be far below that of the ambient. In the field T_L did not differ much from T_a . It seems that the plant did not experience the critical air temperature at which it started to cool its leaves, since on all three sites, T_a did not exceed 40 °C. This temperature seems not high enough to trigger the response that was shown in chapter 3, when T_L became far below T_a at a higher ambient temperature. When Lange (1959) measured *Citrullus* T_L much below T_a he did that at

much higher air temperature than was measured at all the sites in the present study. However, at such high levels of incident solar energy the plant could keep its leaf temperature very close to that of the air by dissipating a large part of the gained heat through λE (Fig. 8.11).

It can be seen from Fig. 8.12, 8.13 and 8.14 that negative values of g_s , E and g_a were calculated in the early morning and late afternoon just before and after the sunset yet no condensation was observed. Clearly this is physically impossible. At very low solar angles the determination of radiation absorbed is not reliable, as mismatches in angles and positions of leaves and models can cause misleading results: if the models cannot 'see' the solar disc but only the cold sky they will become very cold whereas the leaves in a slightly different position may receive direct insolation and thus become warmer. Moreover, the quantum sensor was held above the canopy and not therefore subjected to the leaf shading in exactly the way the leaves and models may be, at least at these low solar angles. Furthermore, inspection of equation 2.6 and 2.7 in chapter 2 shows that the calculated quantities C and λE become indeterminate when R_n tends to zero.

Values of T_L^* lower than T_L should not occur. Such results were however recorded during the early and late parts of the day (Fig. 8.8, 8.9 and 8.10). This might be caused by a substantial lag between the temperatures of the upper and lower surface of the models, resulting from their considerable thickness. Sometimes the junctions fell off, particularly in the early morning, if the glue was insufficient.

Maximum g_s values of *C. colocynthis* were measured in early morning at all sites. In the controlled environment the plant had a maximum g_s higher than those measured in the field. But generally the field values of g_s were higher than those measured indoors for ambient temperatures below 40 °C (Fig. 3.7). However, the trend of g_s in the outdoor measurement is different from that in the controlled environment for well watered and younger plants. In the field in late summer, plants might be vulnerable to water stress especially during midday. Thus they might exhibit a different trend of stomatal conductance. Having an early maximum g_s could be a result of low water stress and VPD at that time of day. The response of g_s to VPD can be assessed from Fig. 8.17. Although it seems that g_s may decrease as VPD increases, this conclusion is not clear and this response of the plant needs further study over a greater range of VPD. However, the coastal site did display the low VPD in the early morning and the highest conductance later, while in the wadi site the plant exhibited low VPD and high g_s most of the day comparing to the other site. On the contrary, at the desert site, g_s was high most of the morning with a high VPD during all the day. The increase of g_s at low VPD is reported by numerous workers but does not occur in all species (see e.g. Schulze et al., 1972; Hall, Schulze & Lange, 1976; Osonubi & Davies, 1980; Willmer, 1983).

High values of g_s in the morning, comparable to those reported here, were observed in other deserts on *Phragmites communis* (Pearcy et al., 1974), *Hyptis emoryi* (Smith & Nobel, 1977b) and *Rhamnus californica* (Williams, 1983).

The independence of g_s and E can be seen from Fig. 8.12 at the coast site, whereas g_s seems to decrease from early in the morning, E was increasing over the same period. This pattern of response was reported for other species (Jarvis & Morison, 1981). Jarvis and Morison (1981) pointed out that it is only under water stress conditions that g_s becomes dependent on E , as the high rate of E causes a low leaf water potential, which if low enough, will eventually cause g_s to be reduced; while in the desert (Fig. 8.13) and wadi site (Fig. 8.14) E and g_s are closely associated.

E was increasing with the solar energy increase reaching a maximum rate at midday as was shown in Fig. 8.18 except in a few cases when a sudden decrease or increase of E occurred. These minor variations were associated with, and presumably caused by, variations in g_s . Any association between g_s and E does not necessarily imply a causal or controlling link. The extent to which E is controlled by climatological versus stomatal characteristics is discussed in a later chapter.

High g_a in the desert site was measured in early morning when strong wind was blowing, though unfortunately it was not possible to measure its speed. In the afternoon the wind speed noticeably decreased. In the wadi site, maximum g_a was in the late afternoon when high wind speed was prevailing (Fig. 8.15). It was noteworthy that at both sites in the afternoon, g_a was increasing while g_s was decreasing. At this time, the plant was able to dissipate the excessive absorbed energy by λE while boundary layer conductance was low. But when E decreased the other means of dissipating the heat load

was to exchange the sensible heat with the ambient, associated with the high g_a . Such a high g_a was caused by the high prevailing wind speeds which are probably a feature of such desert sites. As the sensible heat removal from the plant leaves increases, the energy required for evaporating water decreases which leads to a low E (Jarvis, James & Landsberg, 1976; Grace, 1981). In the coastal site the wind speed during the day did not cause large differences between g_a values in the morning and the afternoon.

A high g_a is bound to have the effect of coupling T_l to the ambient temperature more closely. Thus, transpirational cooling is likely to be an effective process only when wind speeds are low. At high wind speeds the leaf temperature is likely to be close to air temperature. The interplay of g_s and g_a in determining leaf temperature, over the range appropriate for *Citrullus*, will be considered quantitatively in chapter 9.

CHAPTER 9

GENERAL DISCUSSION AND CONCLUSIONS

9.1 Surface resistances and cooling

It was shown in Chapter 3 that solution of the leaf energy balance yields a reliable estimate of the transpiration rate E . In practical situations the precision of the estimate is limited by the difficulty in measuring small temperature differences, the uncertainty in knowledge of the radiation flux that the leaf absorbs, and by the sampling intensity. However, these problems are not great in the main part of the day.

In this work it has been confirmed that *C. colocynthis* has the capacity to lower its leaf temperature below that of the ambient. That was made clear in the experiment conducted in the controlled environments (Fig. 3.6 and Fig. 5.2). However, in the latter case, the cooling started at a low T_a (30 °C) while in the former case cooling was not observed until much higher ambient temperatures were attained (40-44 °C). The two data sets were obtained in different growth cabinets with different energy fluxes. In the field such cooling was not measured as was shown in Chapter 8. Leaf temperatures obtained in the field in the present study were nothing like those extremes reported by Lange (1959) at the same air temperature. However, other environmental factors need to be considered such as soil moisture, vapour pressure and wind speed. The latter along with the leaf size will reduce g_a , and

a very low g_a is necessary to decouple the leaf temperature from T_a (see below). In the present study, field measurements were done in late summer at a time when the least soil moisture is expected. Moreover, by this time, the newly expanded leaf has become deeply dissected. In the rather windy days that were encountered during the field measurement period, it is expected that T_L will be better coupled to the ambient temperature, than it might have been on windless days, though having a high g_a .

Citrullus exhibited very high rates of transpiration in comparison with other desert plants, but the rates in the field were not as high as those in the laboratory. In the field the rates were up to $0.16 \text{ g m}^{-2}\text{s}^{-1}$ whilst in the laboratory they were two or three times this value (Figs. 3.7a and 3.8). Lange (1959) reported E for *C. colocynthis* to be $0.15 \text{ g m}^{-2}\text{s}^{-1}$. The high values obtained in the controlled environments were for young, well-watered plants. In the desert at late summer it is likely that soil moisture is not sufficient to maintain a high rate of E , nor is a high rate really necessary because the hottest days, by then, are over and the lethal temperature would not be reached.

In the controlled environments *Citrullus* displayed a relatively high g_s (maximum g_s was 0.015 m s^{-1}). In the field, only half that value was obtained. This low stomatal conductance in the field might be caused by the stomatal response to the low soil water content. Response of stomata to a critical soil water status has been reported by some authors. This response involves hormones such as abscisic acid

produced in the root at a critical soil water content and transported to the leaf to control the stomatal aperture (Aspinall, 1980). This is thought to be an adaption for plants under water stress. Gallon, Turner and Schulze (1985) reported for *Nerium oleander* that there is no relation between the leaf water potential and g_s but that there might be a critical soil water content at which conductance decreases. The same response of g_s to soil water depletion was reported by other workers (e.g. Bates & Hall, 1981; 1982; Ehleringer, 1983). However, comparison between stomatal responses obtained in the controlled environment and field measurement should be made with care, as the response might differ due to the different growth conditions (Davies, 1977).

The boundary layer conductance g_a in the controlled environment depended on the wind speed and the leaf posture. g_a was found to range from 0.05 to 0.09 m s^{-1} in the controlled environment with wind speed $< 0.5 \text{ m s}^{-1}$. Much higher g_a was measured under the same wind speed at $T_a = 50^\circ\text{C}$ and this might have been a result of leaf movement. In the wind tunnel experiment, determination of g_a using the cooling curve technique showed an increase in boundary layer conductance as the wind speed was increased. g_a at a wind speed of 4 m s^{-1} was 0.14 m s^{-1} . It was also shown that a change in leaf posture from horizontal to vertical increased g_a resulting in an increase of heat loss.

Comparing g_a values obtained in the controlled environments with those obtained in the field at the same wind speeds we see that g_a is about the same for both sets

of measurements (e.g. it is 0.065 m s^{-1} at wind speed of 2.5 m s^{-1} , Fig. 4.2.4 and Fig. 8.16.)

9.2 Simulation

To clarify the interaction between g_s and g_a and to demonstrate how these conductances influence leaf temperature and transpiration rate, a simulation was carried out. This approach has been used by several workers to study the physical environmental factors and their interaction with the plant resistances or conductances (e.g. Taylor, 1975; Woodhouse, William & Nobel, 1983). Grace (1983) proposed an iterative solution of the leaf energy balance equation (equation 2.6) to predict the transpiration rate and leaf temperature from leaves when stomatal and aerodynamic conductances are known. In the present work the approach outlined on page 59 of Grace (1983) has been used. Equation 2.6 was solved using artificial data as input. The absorbed radiation and stomatal conductances were described by a sine wave function in which the maximum R_n (340 W m^{-2}) and g_s occur at midday, and the daylength was 12 hours. The range of g_s and g_a were based on the observations in the field and laboratory:

$$\begin{aligned} \text{maximum } g_s &= 0.007, 0.015 \text{ m s}^{-1} \\ g_a &= 0.02, 0.04, 0.062, 0.083 \text{ m s}^{-1} \\ T_a &= 35, 40, 45 \text{ }^{\circ}\text{C} \\ e_a &= 20 \text{ mbar (} e_a = \text{water vapour pressure)} \end{aligned}$$

In these calculations it is assumed that there is no effect of VPD on the stomatal conductance (since there was little evidence for this in the data); and that feedback between transpiration and vapour pressure is negligible. The input data contain diurnal variation in radiation only: other variables are held constant to permit us to investigate the interplay of variables in the simplest possible case where interpretation is unequivocal.

Fig. 9.1 shows that both g_a and g_s are important in determining the transpiration rate, and so are the climatological variables. The rather similar magnitudes of g_a and g_s mean that both are important in determining the magnitude of the overall diffusive conductance. This contrasts sharply with some other types of leaves where one part of the resistance chain dominates the other. In conifers, for example, the leaves are so small that the aerodynamic term is generally unimportant and the stomata are particularly effective in controlling transpiration. At the other extreme, in certain large-leaved tropical trees like *Tectona grandis* the boundary layer is thick and the aerodynamic term is so important that the stomata may not be very important at all, at controlling E. In *Citrullus* aerodynamic changes in leaf dissection and posture will indeed influence transpiration and hence surface temperature, and stomatal movements can also be used to regulate water loss and leaf temperature.

The leaf temperatures corresponding to these transpiration rates are plotted in Fig. 9.2. The most efficient cooling occurs when g_a is low and g_s high. The computed T_L is

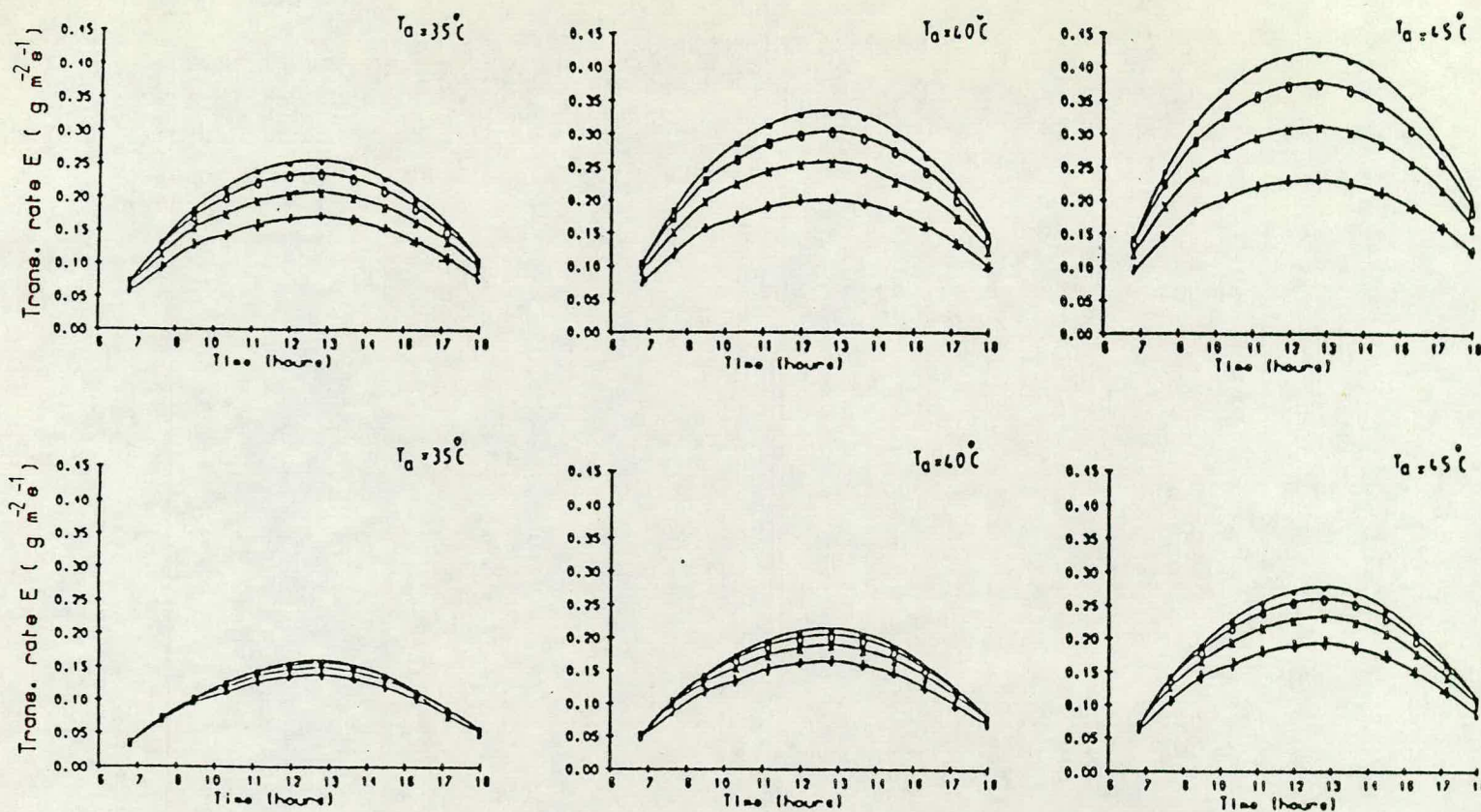


Fig. 9.1 The computed transpiration rate E ($\text{g m}^{-2} \text{s}^{-1}$) at different g_a values; 0.08 (\circ), 0.062 (\bullet), 0.04 (\times), 0.02 ($+$) m s^{-1} . The upper row is for high g_s (0.015 m s^{-1}) and the lower row for low g_s (0.007 m s^{-1}). Vapour pressure e_a was 20 mbar.

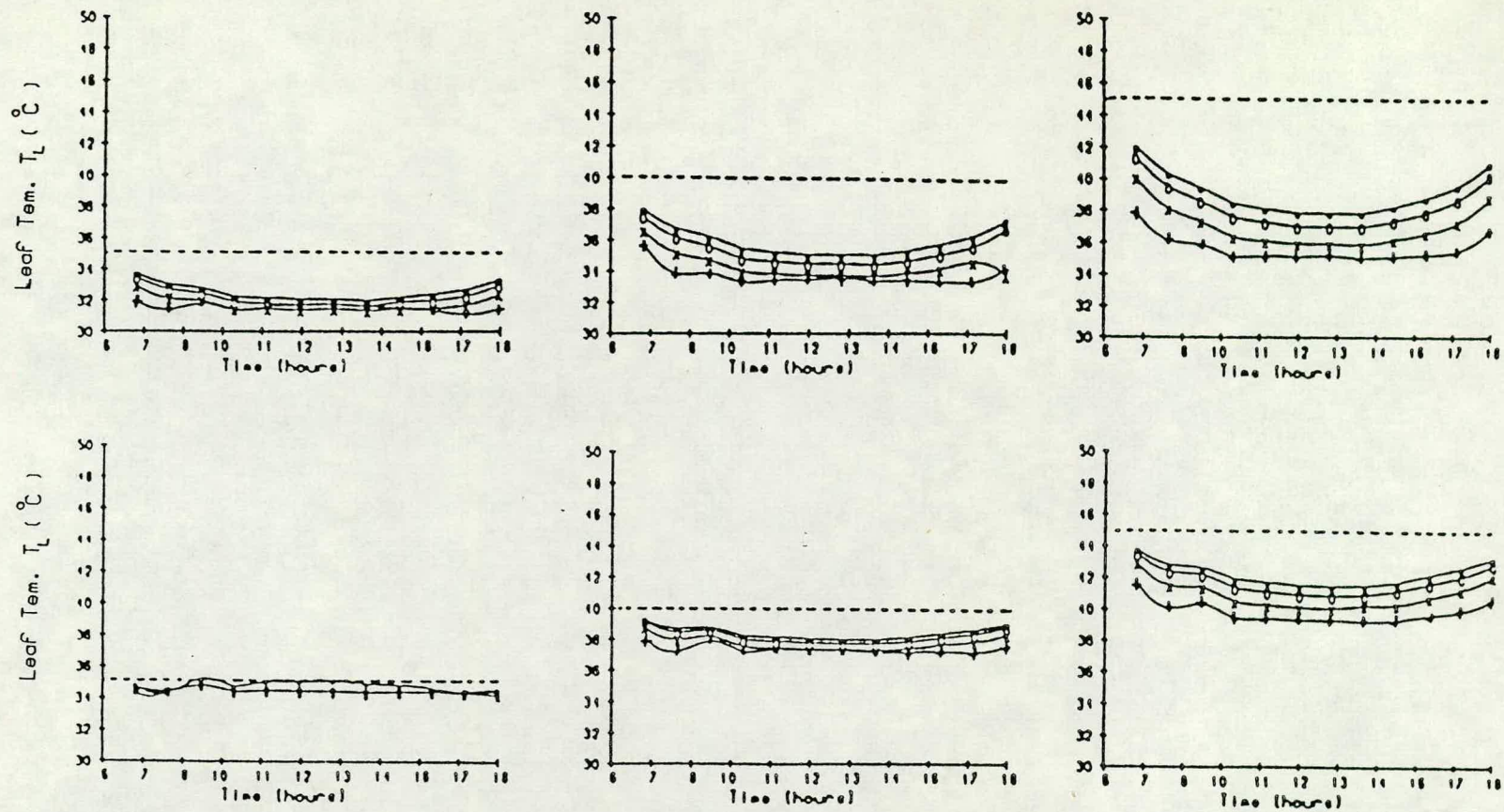


Fig. 9.2 The computed leaf temperature T_L as a function of g_a (g_a values were 0.083 (\circ), 0.062 (\diamond), 0.04 (\times), 0.02 ($+$) m s^{-1}). The upper row is for a high g_s (0.015 m s^{-1}) and the lower row for a low g_s (0.007 m s^{-1}). The dashed line denotes the air temperature.

strongly dependent on humidity and is not far from what really has been measured at the same ambient temperature (Fig. 5.2). It can be seen that more extreme cooling is expected in still air or low g_a . It may be that Lange (1959) had widely cited measurements under these conditions, because on other days he did not obtain the same magnitude of leaf cooling as mentioned in Chapter 1.

From the foregoing, it can be said that it might be an important strategy for *Citrullus* to grow relatively large leaves in the part of the season when soil moisture is abundant. In the field high soil moisture becomes available after the rainy season in the spring and early summer. At the end of the summer, soil moisture decreases, producing a more dissected leaf which will increase g_a , and T_L will become more coupled to T_a and certainly never become much higher than T_a . In this respect it might be of significant value concerning the dissipation of heat from a desert plant with a relatively large leaf to possess this large leaf when the soil moisture content is high and the air temperature is high as well so most of the absorbed energy can be dissipated through latent heat. In the late summer during the dry season it is better for the plant to have a small leaf. Some desert plants have notable and obvious seasonal changes in leaf morphology, bearing large leaves in the wet season and small ones in the dry season (e.g. Smith & Nobel, 1977a).

It is also useful to explore the effect of water vapour pressure in the transpiration rate and extent of cooling (Fig. 9.3). For this purpose the absorbed radiation flux R_n was set

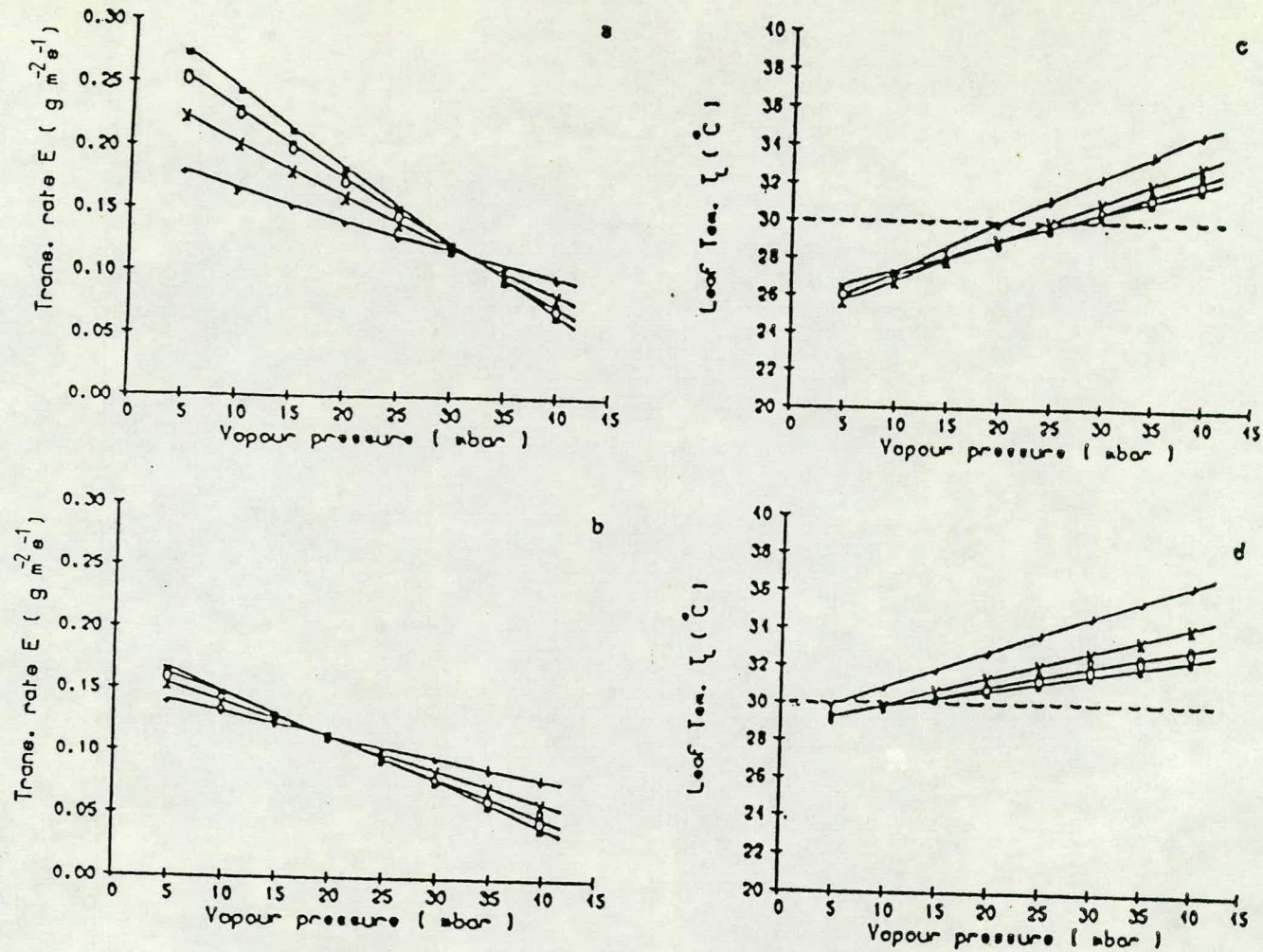




Fig. 9.3 The effect of the vapour pressure on the transpiration rate (a and b) and leaf temperature (c and d) at different g_s values; 0.083 (∇), 0.062 (\square), 0.04 (\times), 0.02 ($+$) m s^{-1} . The upper row for high g_s (0.015 m s^{-1}) and the lower row for low g_s (0.007 m s^{-1}). The dashed line shows the air temperature. Normal range of vapour pressure in the desert 20-30 mbar.

at 340 W m^{-2} . A high g_a increases E at low vapour pressure, but at high vapour pressure decreases it (Fig. 9.3a). This anomaly at high vapour pressure (i.e. nearly saturated air) occurs because the low- g_a leaves heat up more than the high- g_a leaves, so their leaf-to-air vapour pressure difference (VPD) increases substantially. However, these high humidities do not normally occur.

9.3 Growth and life cycle

The early stage of growth from seed is rapid and involves the establishment of several shoots (Fig. 6.5 and Table 6.4), and development of a deep-reaching root system (Fig. 6.3). Once the soil moisture was reached, numerous fibrous roots developed (Table 6.1). It seems that leaf growth was retarded during the development of the deep- roots but  as soon as the water table was reached, the leaf growth increased. It is unclear how long-lived the plants are, as ^{not} ~~many~~ studies in the field have  been undertaken. It appears that established plants are mainly several years old, dying back in winter to the root crown at the end of each growing season and after fruit production. Studies of population dynamics using tagged plants in the field would be very useful. It is not even known how often the plant develops from seed, and how long the seed remains viable in nature.

9.4 Hydrological consequences

This species, and others which may have similar characteristics, may be regarded as weeds because they use water which otherwise would be available for crops. In one of the sites (desert), *Citrullus* was abundant on a market garden, where no attempt had been made to uproot it. Crops in the same field had died. Similarly, in irrigation schemes the presence of the plant in a catchment area could diminish the supply of water.

To estimate how much the transpiration rate from the plant has an effect on the soil water content in the desert where water is in short supply, one diurnal curve of E ($T_a = 40^\circ\text{C}$, $g_a = 0.04 \text{ m s}^{-1}$ and high g_s , Fig. 9.1) was chosen to calculate the total consumption of the soil water for the whole day. It was assumed that the plant has a leaf area index of one and that the cover is up to 10 percent (Fig. 9.4). Typically, the annual rainfall in the desert is $<100 \text{ mm}$. Clearly, the plant can be expected to consume a large proportion of the soil moisture in maintaining the high transpiration rate (Fig. 9.4). As irrigation schemes become more widespread in Saudi Arabia it may be necessary to look carefully at the use of water by the indigenous vegetation.

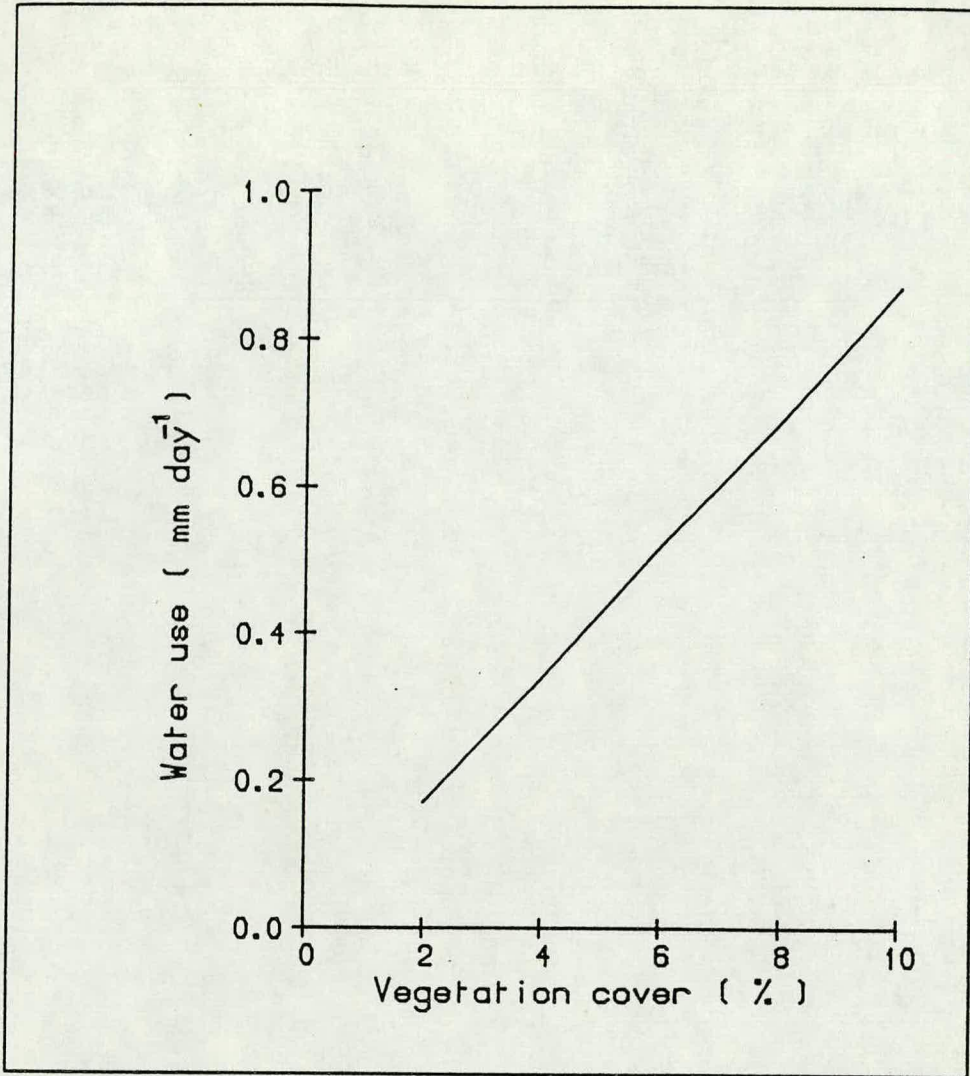


Fig. 9.4 Estimated amount of water used with varying vegetation cover of *Citrullus*.

9.5 Conclusions

1. Surface resistances and transpiration rates may be estimated from measurements of leaf temperature and climatological variables.
2. *Citrullus* leaves display high transpiration rates and frequently have temperatures cooler than the air.
3. In relation to other plants of the desert, the plant displays relatively high stomatal conductance and has a low boundary layer conductance in ordinary conditions.
4. The lethal temperature is rather low in relation to other desert plants, being around 50 °C though some kind of damage does occur at an even lower temperature (46 °C). These temperatures are lower than those achieved during the warmest part of the year in the Saudi Arabian desert. By its high transpiration rate, the plant avoids lethal temperatures.
5. The cooling response is not always displayed. It seems probable that it is only displayed in the hottest part of the year, when water is relatively available. The seasonal control of transpiration can only be elucidated by further studies in the field. Seasonal changes in stomatal and boundary layer conductances are likely to occur.
6. To sustain high transpiration rates, tap roots grow down

to the water-table and fibrous roots are formed in moist zones of the soil.

7. Transpiration rate and leaf cooling is sensitive to radiation interception (which to some extent is under physiological control through leaf movements), stomatal movements, and aerodynamic changes.

8. Further studies in the field are required to see whether *Citrullus* is unique or whether it is just one of an assemblage of species of the Saudi desert which display high transpiration rates.

9. Preliminary calculations suggest that vegetation containing *Citrullus* and similar species may consume significant quantities of water to the detriment of field crops.

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Appendix A: The Fortran program used to calculate leaf energy balance.

```

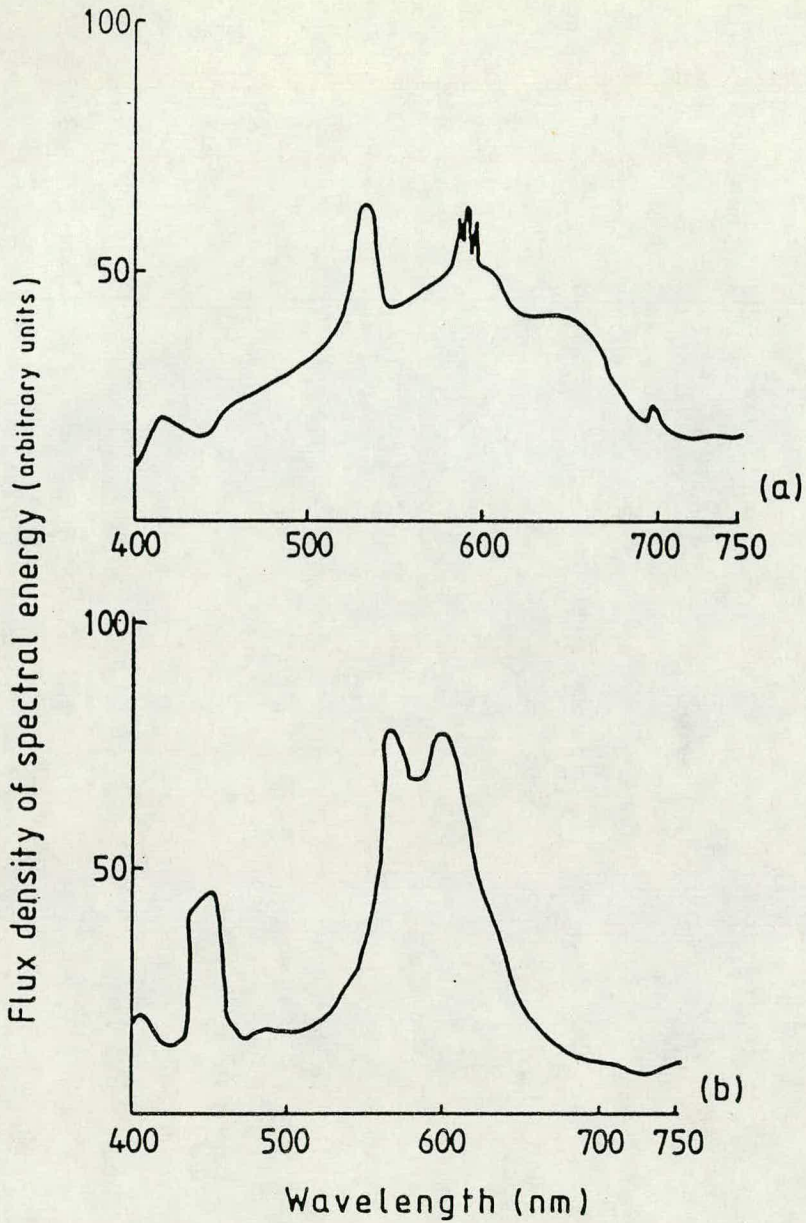
      WRITE(6,2)
2     FORMAT('          C          LE          E          GA
X     GS')
1     READ(5,*)RNTZ,TAZ,TLNTZ,TLTZ,WBDZ
      RTZ=RNTZ
      CALL PENMONT(RNTZ,RTZ,TAZ,TLNTZ,TLTZ,WBDZ,CZ,ZZZ,EZ,RAZ,RSZ)
      GAZ=1/RAZ
      GSZ=1/RSZ
      WRITE(6,100)CZ,ZZZ,EZ,GAZ,GSZ

      GOTO1
100    FORMAT(1H ,5F13.4)
      END

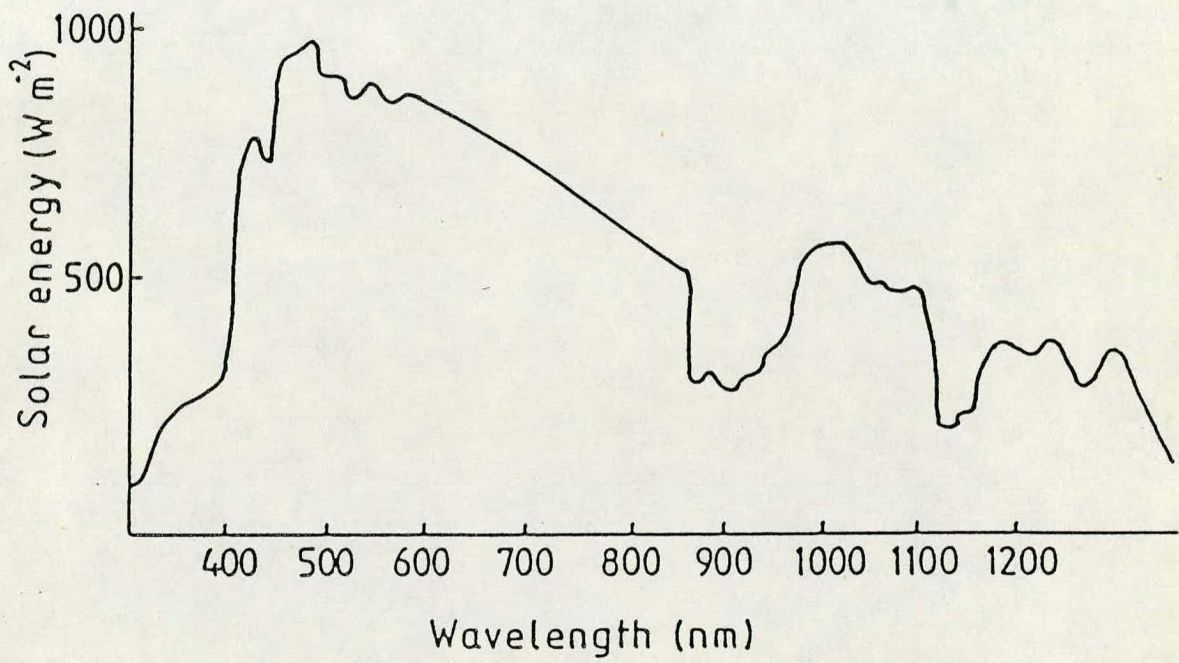
      SUBROUTINE PENMONT(RNT,RT,TA,TLNT,TLT,WBD,C,LE,E,RA,RS)
      REAL*4 A,CS,C,E,EA,EL,GAMMA,LAMBDA,LE,P,RA,RHO,RNT,RS,RT,SIGMA,TA,
      TLNT,TLT,WBD,WBT
      DATA A/6.666E-04/,CP/1.01/,GAMMA/0.66/,LAMBDA/2454./,P/1000./,RHO/
      11150./,SIGMA/5.67E-8/
      RA=(RHO*CP*(TLNT-TA))/RNT
      LE=SIGMA*((TLNT+273.16)**4-(TLT+273.16)**4)-RHO*CP*(TLT-TLNT)/RA
      E=LE/LAMBDA
      C=RT-LAMBDA*E
      WBT=TA-WBD
      EA=SVP(WBT)-A*P*WBD
      EL=SVP(TLT)
      RS=((RHO*CP*(EL-EA))/(GAMMA*LAMBDA*E))-RA
      RETURN
      END

C CALCULATE SATURATED VAP. PRESSURES(MB.) FROM THE NEW GOFF-GRATCH EQN.
      REAL FUNCTION SVP*4(/TEMP/)
      B=TEMP+273.15
      IF(B.LT.273.15)GOTO 1
      SVP=10**((10.79574*(1-(273.16/B))
      !-5.02800*DLOG10(B/273.16)
      !+1.50475E-4*(1-(10**(-8.2969*((B/273.16)-1))))
      !+0.42873E-3*((10**(4.76955*(1-(273.16/B))))-1)
      !+0.78614)
      GOTO 2
1     SVP=10**(-9.09685*(273.16/B-1)
      !-3.56654*DLOG10(273.16/B)
      !+0.87682*(1-B/273.16)
      !+0.78614)
2     CONTINUE
      RETURN
      END

```


Appendix B.1:

The spectral energy of the light in the controlled environment growth cabinets, Fisons Model 2340 (a) and the controlled environments Model EF7, as measured with a scanning quanta spectrometer (QSM-2500).

Appendix B.2:

The spectral distribution of global solar radiation received on a horizontal surface at the ground for an air mass = 1.5.
(Redrawn after Gates, 1980.)

Appendix C.1:

Source of variation	df	sum of squares	mean sum of squares	variance ratio	significance level
Treatment	5	2037.00	407.39	5.25	0.01
Error	24	1859.31	77.47		
Total	29	3896.31			

Analysis of variance for the petiole-to-stem angle for the water-stressed plants.

Source of variation	df	sum of squares	mean sum of squares	variance ratio
Treatment	5	1350.56	270.11	2.56
Error	24	2523.81	105.15	
Total	29	3874.37		

Analysis of variance for the leaf-to-petiole angles for the water-stressed plants. No significant difference at $p=0.05$.

Appendix C.2:

Source of variation	df	sum of squares	mean sum of squares	variance ratio
Treatment	5	820.31	164.06	0.54
Error	24	7288.43	303.68	
Total	29	7288.43		

Analysis of variance for the petiole-to-stem angle for the well-watered plants. There is no significant difference at $p=0.05$.

Source of variation	df	sum of squares	mean sum of squares	variance ratio
Treatment	5	634.43	126.88	1.19
Error	24	2551.37	106.30	
Total	29	3185.81		

Analysis of variance for the leaf-to-petiole angle for the well-watered plants. There is no significant difference at $p=0.05$.

Appendix D:

Source of variance	df	sum of squares	mean sum of squares	variance ratio	p
Treatment	6	94.68	15.94		0.01
Error	28	8.903	0.299		
Total	34	104.029		53.301	

Analysis of variance of Inlog of Potassium leakage.

Source of varaince	df	sum of squares	mean sum of squares	variance ratio	p
Treatment	6	271.51	42.25		0.01
Error	28	1.600	0.057	791.85	
Total	34	273.11			

Analysis of variance of the total leaf survival after the exposure to the different ambient temperatures.

Appendix E: The Fortran program used to calculate the error analysis.

```

      DIMENSION IFREQ1(300),IFREQ2(300),IFREQ3(300)
89      DO 88 I=1,300
          IFREQ1(I)=0
          IFREQ2(I)=0
          IFREQ3(I)=0
88      CONTINUE
      READ(5,*)TIME,RTZM,RMTZ,TAZ,TLMTZ,TLTZ,WBDZ
      F=RTZM/RMTZ
      SHORTDIFF=RTZM-RMTZ
      CALL PENMONT(RMTZ,RTZM,TAZ,TLMTZ,TLTZ,WBDZ,CCZ,ZZZ,EZ,RAZ,
!RSZ,SHORTDIFF)
      GA=1.0/RAZ
      GS=1.0/RSZ
      WRITE(6,100)TIME,CCZ,ZZZ,EZ,GA,GS

      E1=EZ
      GA1=GA
      GS1=GS
      WMLOW=RMTZ*0.85
      WMSTEP=RMTZ*0.05
      ATLOW=TAZ-0.5
      ATSTEP=0.2
      T1LOW=TLMTZ-0.5
      T1STEP=0.2
      T2LOW=TLTZ-0.5
      T2STEP=0.2
      DPLOW=WBDZ*0.85
      DPSTEP=WBDZ*0.05
      DO 16 I=1,7
          WMNOW=WMLOW+(FLOAT(I)*WMSTEP)
      DO 16 J=1,5
          ATNOW=ATLOW+(J*ATSTEP)
      DO 16 K=1,5
          T1NOW=T1LOW+(K*T1STEP)
      DO 16 L=1,5
          T2NOW=T2LOW+(L*T2STEP)
      DO 16 M=1,7
          DPNOW=DPLOW+(FLOAT(M)*DPSTEP)
      RTZ=WMNOW+SHORTDIFF
      CALL PENMONT(WMNOW,RTZ,ATNOW,T1NOW,T2NOW,DPNOW,CCZ,ZZZ,EZ,RAZ,
!RSZ,SHORTDIFF)
      GANOW=1.0/RAZ
      GSNOW=1.0/RSZ
C      WORK OUT PROPORTIONATE ERRORS
      AERR=GANOW/GA1
      SERR=GSNOW/GS1
      EZERR=EZ/E1
C      MULTIPLY ERROR BY TEN AND ROUND OFF
      TO CLASSIFY INTO 10-PERCENTILES
      IQ2=IFIX(SERR*10)
      IQ3=IFIX(EZERR*10)
      IF(IQ1.LT.1)IQ1=1
      IF(IQ2.LT.1)IQ2=1
      IF(IQ3.LT.1)IQ3=1
      IF(IQ1.GT.299)IQ1=300
      IF(IQ2.GT.299)IQ2=300
      IF(IQ3.GT.299)IQ3=300
      IFREQ1(IQ1)=IFREQ1(IQ1)+1
      IFREQ2(IQ2)=IFREQ2(IQ2)+1
      IFREQ3(IQ3)=IFREQ3(IQ3)+1
16      CONTINUE
      DO 50 I=1,50
50      WRITE(6,101)IFREQ1(I),IFREQ2(I),IFREQ3(I)
100      FORMAT(1H ,6F13.4)
101      FORMAT(1H ,3I10)
      GOTO 89
      END

```

Cont./...


```

SUBROUTINE PENMONT(RMT,RT,TA,TLMT,TLT,WBD,CC,LE,E,RA,RS,SHORT)
REAL*4 A,CS,CC,E,EA,EL,GAMMA,LAMBDA,LE,P,RA,RHO,RMT,RS,RT,SIGMA,TA,
1 TLMT,TLT,WBD,WBT
DATA A/6.666E-04/,CP/1.01/,GAMMA/0.66/,LAMBDA/2454./,P/1000./,RHO/
11150./,SIGMA/5.67E-8/
RA=(RHO*CP*(TLMT-TA))/RMT
CC=(RHO*CP*(TLT-TA))/RA
LE=RT-CC
E=LE/LAMBDA
WBT=TA-WBD
EA=SVP(WBT)-A*P*WBD
EL=SVP(TLT)
RS=((RHO*CP*(EL-EA))/(GAMMA*LAMBDA*E))-RA
RETURN
END

```

C CALCULATE SATURATED VAP. PRESSURES(MB.) FROM THE NEW GOFF-GRATCH EQN.

```

REAL FUNCTION SVP*4(/TEMP/)
B=TEMP+273.15
IF(B.LT.273.15)GOTO 1
SVP=10**((10.79574*(1-(273.16/B)))
!-5.02800*DL0G10(B/273.16)
!+1.50475E-4*(1-(10**(-8.2969*((B/273.16)-1))))
!+0.42873E-3*((10**((4.76955*(1-(273.16/B)))))-1)
!+0.78614)
GOTO 2
1 SVP=10**((-9.09685*(273.16/B-1)
!-3.56654*DL0G10(273.16/B)
!+0.87682*(1-B/273.16)
!+0.78614)
2 CONTINUE
RETURN
END

```